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SEASONAL CHANGES IN THE ATTACHED ALGAE OF FRESHWATER AND SALINE LAKES IN THE LOWER GRAND COULEE, WASHINGTON[1]

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ABSTRACT

A two year investigation of two freshwater alkaline lakes and two saline lakes in the Lower Grand Coulee has provided a quantitative and qualitative record of many of the seasonal changes occurring in the non-planktonic algae. A glass plate method satisfactorily recorded quantitative changes in the attached algae. The plates (28 by 28 cm) were submerged for 2 to 4 weeks at various depths. Dry weight and ash-free dry weight of the predominantly algal attachment materials on plates were determined, and the ash-free weight was expressed as a production rate. The ash from freshwater lakes was composed normally of intact diatom frustules. The ash from saline lakes was also diatomaceous, but the weakly silicified frustules were deformed during ashing. Proportional counts of the various species in freshwater lakes were made using the ash. The evaluation of relative dominance was based on the mathematical product of the cell count and a calculated volume factor for each species. The glass-plate production technique was examined at some length and it was concluded that a 2-week submergence period was most satisfactory, that glass was not unduly selective, that a horizontal position was satisfactory, and that the method was best suited to the freshwater lakes.

In freshwater lakes (200–450 ppm T.D.S.) results clearly show a bimodal production curve with the peak generally higher in the spring than in the fall. Lowest production invariably occurred in late summer. High production values in the spring were commonly near or above 500 mg/m^2/day. Comparison of the results of two years shows sizable differences in total production at comparable times of year, but the seasonal distribution of species followed the same general pattern both years. *Cymbella affinis, C. cistula, C. mexicana, Diatoma elongatum, Fragilaria vaucheriae, Gomphonema eriense, Nitzchia* spp., *Synedra acus,* and *S. ulna* were characteristic spring dominants in the freshwater lakes. These diatoms were replaced in summer mainly by *Epithemia sorex, E. turgida,* and *Rhopalodia gibba.* A few "spring" species were common in one lake in summer but only at greater depths. The

[1] This study is a revision of part of a thesis submitted to the Department of Botany, the State College of Washington in partial fulfillment of the requirements for the Ph.D. degree.

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The study was assisted in part by a grant from the Jessup Fund of The Academy of Natural Sciences of Philadelphia to which the author is indebted.

Voucher specimens of almost all algae collected are preserved in the author's personal collection. Permanent slides of most of the diatoms collected will be deposited soon in the collection of The Academy of Natural Sciences of Philadelphia.

With the exception of Alkali, Alcove, and Talus, the lake names are those used by Bretz (1932). Alkali, a recently formed lake, is the name used on Bureau of Reclamation maps. Alcove Lake and Talus Lake have previously borne no names (Fig. 1).

summer period was also characterized by a great abundance of *Cladophora, Spirogyra, Oscillatoria,* and members of the Chlorococcales. The dominant summer diatoms usually remained through the fall and were joined at that time by several of the "spring" species. In winter diatom production was generally low, but *Ulothrix* clothed rocks in Falls Lake even under an ice cover.

Nine per cent of the 275 algal taxa collected in the Lower Grand Coulee occurred in both freshwater and saline lakes. Although the saline lakes were not rich in numbers of species, production rates were similar to and even higher than production rates in the freshwater lakes. In the two saline lakes (Lake Lenore—10,000 ppm and Soap Lake—25,000 ppm) there was a pronounced diatom pulse in the fall. Production rate values as high as 550 $mg/m^2/day$ were achieved during this season. In Soap Lake a winter pulse reached a value of 1000 $mg/m^2/day$ which was followed by a distinct spring pulse, both absent in Lake Lenore. The dominants on glass plates in both lakes were species of *Nitzschia* and *Amphora.* Blue-green algae were also common and were conspicuous for their lack of seasonality.

INTRODUCTION

The description of freshwater algal periodicity and the study of the causes of bimodal, unimodal, or apparently erratic seasonal production curves have had a long history, yet no entirely convincing solutions have been proposed. Most studies have been on phytoplankton, and relatively little effort has been expended in analyzing the periodicities of the vastly more numerous species of the non-planktonic algal assemblages, freshwater or marine. Nor has the contribution of the non-planktonic algae to the total primary production of a lake or pond been satisfactorily evaluated.

The present investigation has attempted to develop a satisfactory quantitative method for measuring the changes in attached algae. For a period from December, 1954, to November, 1956, submerged glass was used as a removable substrate for measuring attachment and growth of normally epilithic and epiphytic algae. This was a part of a general floristic and ecological survey of certain freshwater and saline lakes in the Lower Grand Coulee of central Washington.

The algae of lakes in the northwestern United States have rarely been investigated. Previous published research on algae in the Columbia Basin of Washington is limited to studies of the seasonal periodicity of phytoplankton in two of the saline lakes in the Lower Grand Coulee (Anderson 1958, and Anderson *et al.* 1955).

The Grand Coulee runs in a northeast to southwest direction for about 80 km, extending from Grand Coulee Dam on the Columbia River to the city of Soap Lake. It is the most spectacular part of the widespread channeled scablands formed during the Pleistocene by outwash rivers from ice-dammed lakes. A detailed and interpretative geological description of the Grand Coulee is given by Bretz (1932).

The Lower Grand Coulee is a deep gorge with vertical walls 120 to 300 m in height and with a maximum width of almost 2 km (Fig. 1). The trench, extending about 27 km from Coulee City to Soap Lake, was cut by the recession of a cataract. The walls and floor consist of basalt with small numbers of granitic boulders.

The Lower Grand Coulee lies in a semi-desert belt in which the *Artemisia tridentata/Agropyron spicatum* association is predominant (Daubenmire 1942). The annual precipitation is about 8 inches, most of which occurs in fall, winter, and spring. The annual snowfall is about 18 inches. Summer is characterized by clear warm days. The mean temperatures for January and July are about –3°C and 25°C, respectively.

The series of natural lakes in the Lower Grand Coulee is of particular interest in that it shows a considerable salinity gradient, increasing from north to south. The lakes originated in late Pleistocene after the Columbia River regained its present course and the flow of water through the Grand Coulee ceased. Falls, Castle, Deep, Perch, Park, Blue, and Alkali lakes (Fig. 1) may be classified as freshwater, although the total dissolved solid content (T.D.S.) ranged from 200 to over 400 ppm. According to

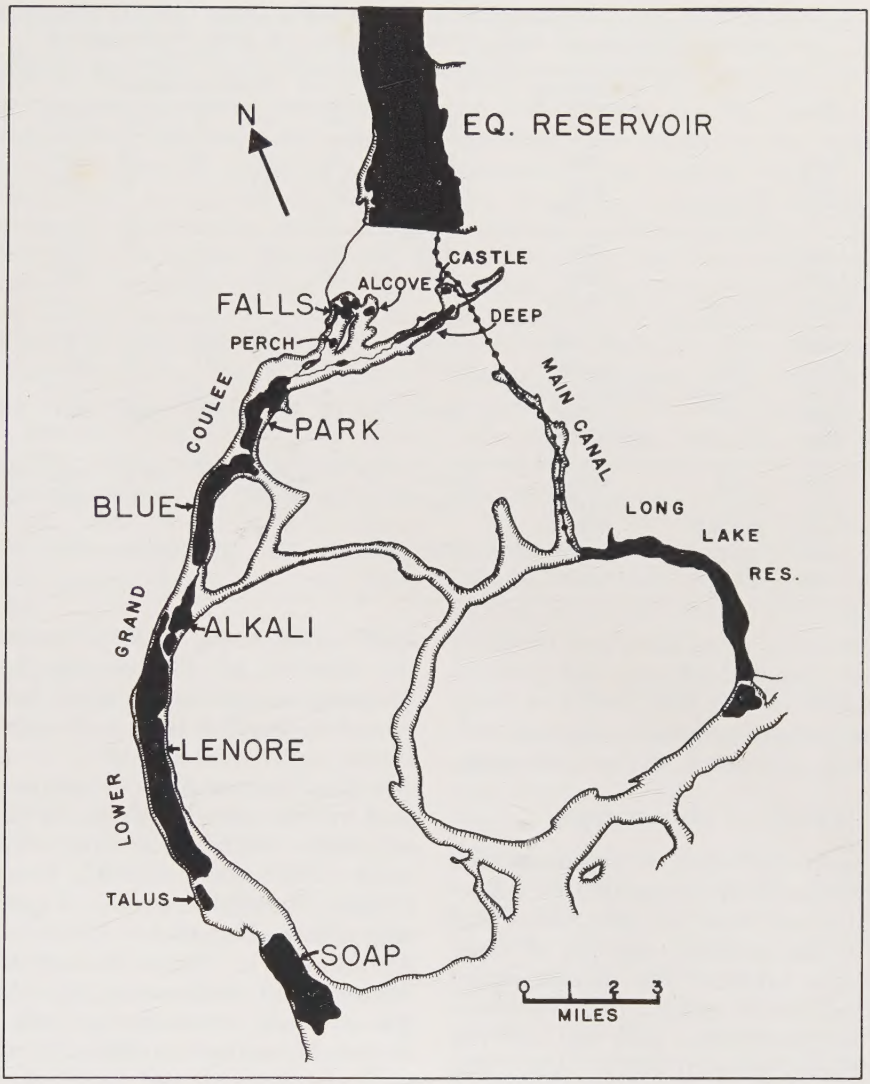

FIG. 1. Sketch map of Lower Grand Coulee area based on Reclamation Service map R_2-4045-3.

Rawson and Moore (1944) such waters could be classified as saline. However, these lakes stand in contrast to the closed waters of Lake Lenore, Talus Lake, and Soap Lake (Fig. 1) in which the T.D.S. content of surface waters ranged from about 8,000 to over 25,000 ppm. In these highly saline lakes the metazoan fauna is limited to a few species of rotifers, microcrustaceans, and insects. Whittaker and Fairbanks (1958) discuss the copepod fauna of these and other Columbia Basin lakes.

Sodium, magnesium, calcium, and bicarbonate are the most abundant ions of the freshwater lakes (Table 1). The predominant ions of the saline lakes are sodium, bicarbonate, and carbonate with lesser amounts of potassium, magnesium, sulfate, and chloride (Table 1).

Recent changes include a rather rapid dilution of the saline waters. This is caused principally by a pumping out of excess water from Lake Lenore and Soap Lake to counteract the rising water level. A rising water table is a widespread phenomenon in the region of the Columbia Basin Project.

TABLE 1. *Conductivity, pH, and concentration of dissolved solids of Lower Grand Coulee surface waters; data in italics from present study, other data from U. S. Dept. of the Interior*

Water	Year	pH	Conductivity, micromhos @ 25°C	Parts per million								
				T.D.S.	Ca	Mg	Na	K	CO_3	HCO_3	SO_4	Cl
Falls	1954	–	398	244	24	17	33	6	12	185	24	9
Lake	1956	–	415	300	22	19	33	7	0	203	30	11
	55–56	*8.0–9.1*	*370–407*	–	–	–	–	–	–	–	–	–
Alkali	1955	–	678	440	13	24	105	12	0	367	34	20
Lake	1956	–	556	356	18	22	71	13	0	291	30	15
	55–56	*8.4–9.4*	*674–539*	–	–	–	–	–	–	–	–	–
Lenore	1949	9.7	23,206	18600	9	20	6969	508	3990	4636	2923	1856
Lake	1954	9.8	14,158	11040	8	20	3887	321	1746	3221	1627	1093
	1955	*9.5–9.6*	*11,528–12,388*	–	–	–	–	–	–	–	–	–
	1956	9.7	10,640	7500	5	15	2622	239	936	2885	1378	724
	1956	*9.5–9.7*	*10,000–11,217*	–	–	–	–	–	–	–		–
Soap	1949	9.8	43,000	38954	5	17	14260	739	7440	6893	6960	5183
Lake	1954	10.0	30,087	25440	8	20	8763	774	4050	5020	4560	3444
	1955	*9.5–9.7*	*27,666*	–	–	–	–	–	–	–	–	–
	1956	10.0	24,980	20600	5	16	7291	602	3360	3788	3782	2570
	1956	*9.7–9.8*	*24,774–26,774*	–	–	–	–	–	–	–	–	–

The sixteen or more lakes and ponds in the Lower Grand Coulee are not polluted to any extent at this time, but it is likely that some forms of pollution will occur with a constantly increasing recreational usage.

MATERIALS AND METHODS

The regular collection of non-planktonic algae included both a quantitative collection of attached algae on glass plates and a more or less random sampling of algae from all lake habitats. The present report is restricted almost entirely to a consideration of the quantitative data and will not give a detailed account of the algal flora. A full account is available in typescript at the Science Division, Holland Library, State College of Washington (Castenholz 1957).

The measurement of production rate

A quantitative sampling method which employed submerged glass plates was used for a two-year period. The method involved submergence of the plates in a horizontal position for a fixed period of time, removal of attachment materials by scraping, and determination of dry weight followed by a determination of weight lost on ignition. This method is essentially a modification of the technique used by Newcombe (1949, 1950). Newcombe (1950), working for a few months in a Michigan lake, used 18 standard microscope slides horizontally placed in wooden racks and suspended at various depths from buoys.

A glass slide or plate technique was also used in freshwater by Abdin (1949), Butcher (1932a, 1932b), Cholodny (1930), Godward (1937), Ivlev (1933), Patrick *et al.* (1954), Thomasson (1925), Yount (1956), and others. Bissonnette (1930), Coe and Allen (1937), Hentschel (1916, 1925), Scheer (1945) and several others have used glass to study attachment, growth, and succession in marine situations. The general methods are reviewed by Cooke (1956). Many of the workers have utilized direct microscope counts of organisms attached to slides. Such a method fails when growth becomes so heavy that it cannot be fractionated *in situ* under the microscope. This was generally the case with the submergence period of two weeks used in the present study. Newcombe, on the other hand, considered only the production of total organic matter and gave no consideration to the species composition. The present study has sought to combine a method of estimating production rate in terms of ash-free weight with a method of estimating the species composition of the attachment materials.

Square plates (28 by 28 cm) of double strength glass were placed in the lakes. In most locations the plates were placed directly on the rock substrate. Such plates had a single drilled hole and were attached to an object on shore by means of a wire line. Other plates in regions of unstable bottom material or of heavy wave action were fitted with 3 holes and mounted on 3 rubber cups of a standard automobile top-rack type. Thus, the plate was above the substrate by a few centimeters and breakage or heavy silting was usually prevented. The motive in placing plates directly on the substrate, instead of suspending them from buoys in open water, was to have the artificial substrate as close as possible to the origin of the "seed" of the epilithic algae. Whether a measurable lag in "seeding-on" would occur offshore has not been determined.

At the stations in all lakes, plates were located at approximately 0.4 m depth. In Falls Lake plates were also located very close to the surface, and during the summer at depths of 1, 2, and 3 m. The deeper plates were placed and retrieved by diving. The depth of plates was kept fairly constant by adjustment at every visit. Throughout the study, plates were exposed for either a 2-week or a 4-week period. The attachment material was removed from the plates with a steel carpenter's scraper with a straight edge. Both sides of the plates were scraped but generally only material from the top side was collected except when tripod mounts were used. The material from each plate was collected in a wide mouth jar and preserved with a small amount of formalin immediately after collection. In most cases the scraped plates were replaced in position after washing in lake water. Generally only a few minutes elapsed between scraping and washing and thus the plates were seldom dried. In some cases unused plates were used as replicates.

The collected material was then examined microscopically in the laboratory and an estimate of the relative abundance of each species was made. It was then oven-dried at 105°C for 24 hours in tared porcelain crucibles and allowed to come to equilibrium in a desiccator. Following the dry weight determination the material was ashed at 650°C for one hour in a muffle furnace. The ash-free dry weight (loss on ignition) was taken as an approximate measure of the organic weight. Ash-free dry weight is a practical quantity which represents mostly organic matter. Carbon dioxide is also lost from alkaline earth carbonates and from some alkali bicarbonates, but generally at higher temperatures only. Carbonates probably occur on glass plates mainly as inorganic sediments which were present usually in small amounts. In any case essentially inorganic sediments of Lower Grand Coulee lakes were ashed with less than 5% loss of weight.

The results are expressed as mg of ash-free dry weight produced/m^2/day (Figs. 2–10 and Tables 4–5). The date chosen for plotting is the mid-date of the submergence period.

The species composition

Almost all of the ash from the freshwater attachment material was composed of intact diatom frustules. This ash was suspended uniformly in water by vigorous shaking, pipetted onto slides, and dried to a uniform film. Permanent mounts were made with hyrax medium. The addition of hyrax did not appear to alter the uniformity of the diatom spot.

The ash from saline lakes was also composed primarily of diatom wall material. However, the walls of these diatoms were weakly silicified and were greatly deformed during ashing. The ash developed a glazed crust and uniform suspensions and counts could not be made.

Proportional counts of the freshwater material were then made under a ×100 oil immersion lens with ×10 oculars, using a Whipple ocular micrometer grid. Random grid fields were counted until the total number of cells amounted to 300 usually. By making several counts of 1,000 cells or more for different samples it was found that 300 gave reasonable statistical accuracy in most cases. In some instances only 100 cells were needed, and occasionally 600 were necessary.

The number of cells of each species was tabulated. All species that occurred more than once were included in subsequent calculations.

Since the production rate of the total attachment material was expressed in weight, it is obvious that the number of cells of species which differ considerably in volume would not lead to an accurate expression of dominance in biomass. For this reason the relative cell volumes were calculated. Even though the ratio of silica wall weight to organic weight would undoubtedly change with increasing or decreasing volume, relative volume appears to be the only practical factor to combine with cell numbers of species to approximate a quantity of the biomass collected.

Volume calculations were made by making camera lucida drawings of the largest and smallest cells encountered of each species. Valve views and girdle views of the same length were drawn. The relative areas of valve views of different species were determined by using a Keuffel and Esser planimeter. The areas of girdle views were similarly determined and divided by length to arrive at the third dimension with which to calculate volume. The problem of length in girdle view is not difficult to solve, since the ends are usually truncate. Thus, the value area was multiplied by the mean width of girdle view, this for both minimum and maximum sizes. The mid-volume value was used on a relative scale for the various species. The species with the smallest volume was given a value of one; all other species were given values relative to this (Table 2). It may be seen that the volume of the largest species (*Cymatopleura solea*) was 804 times the volume of one of the smallest (*Acnanthes minutissima*) (Table 2).

The cell count for each species was multiplied by the respective volume factor. The products obtained in this manner were totaled, and percentages of the total were determined for each species. The percentages thus obtained were plotted as a fraction of the ash-free dry weight expressed as a production rate for each plate sample (Figs.

TABLE 2. *Relative cell volumes of diatom taxa occurring on glass plates in fresh-water lakes*

Taxon	Volume	Taxon	Volume
Acnanthes minutissima	1	*Gomphonema* sp. "A"	6
Amphora ovalis	42	*Melosira italica*	2
A. ovalis v. *pediculus*	1	*Navicula cryptocephala*	2
A. sp. "A"	1	*N. cuspidata*	52
Cocconeis pediculus	8	*N. gregaria*	2
C. placentula	8	*N. lanceolata*	3
Cyclotella meneghiniana	6	*N. oblonga*	192
Cymatopleura solea	804	*N. radiosa*	16
Cymbella affinis	15	*Neidium iridis*	69
C. cistula	79	*Nitzschia amphibia*	4
C. mexicana	388	*N. angustata*	24
C. microcephala	1	*N. dissipata*	4
C. turgida	67	*N. frustulum*	3
C. ventricosa	8	*N. gracilis*	1
Diatoma elongatum	7	*N. linearis*	6
Epithemia sorex	16	*N. palea*	3
E. turgida	349	*Rhoicosphenia curvata*	16
E. zebra	36	*Rhopalodia gibba*	135
Fragilaria brevistriata	1	*Stauroneis phoenicenteron*	76
F. capucina	3	*Stephanodiscus astraea*	1
F. construens	1	*S. niagarae*	130
F. vaucheriae	3	*Surirella ovata*	43
Gomphonema constrictum	14	*Synedra acus*	8
G. eriense	22	*S. mazamaensis*	1
G. intricatum	2	*S. rumpens*	5
G. olivaceum	6	*S. ulna*	87
G. parvulum	3		

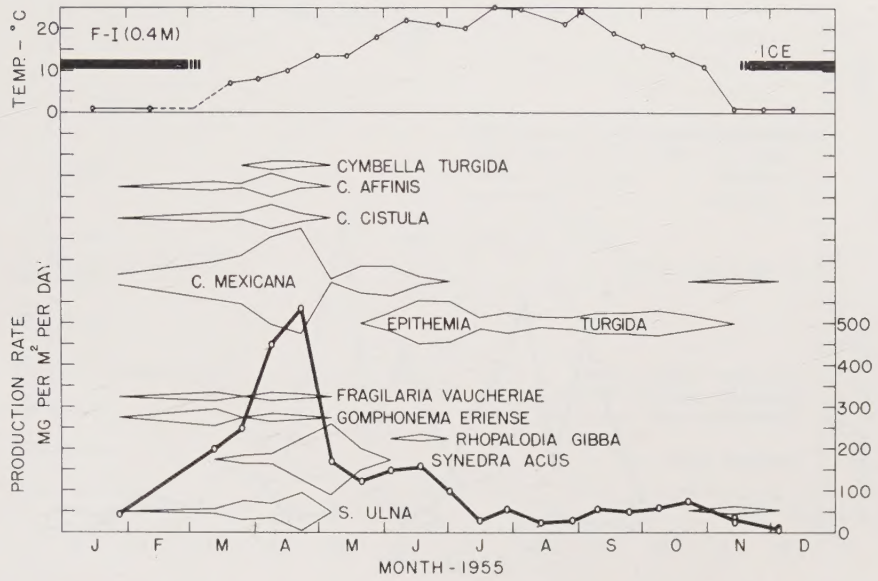

FIG. 2. Falls Lake F-I (0.4 m) *1955*: production rate on glass as ash-free dry weight, the diatom species composition, and temperature and ice data. Mid-dates of submergence periods are used.

2–8). This technique evaluates the contribution in biomass of different species to the whole production of organic matter. Unfortunately, with the scale used in the graphical representation it was impractical to take into account many of the smaller celled species whose calculated contributions do not exceed 5 mg of ash-free dry weight/m^2/day. Thus, the technique as here practiced does not succeed in comparing the growth rates of species of all cell sizes. Another difficulty is the fact that in the freshwater lakes many of the important epilithic diatoms are attached by elongate "gelatinous" stalks (*e.g., Cymbella, Gomphonema*) while others are attached by short "gelatinous" pads or by an entire side of the frustule (*e.g., Synedra, Epithemia, Acnanthes*). The presence of the extracellular organic matter in a mixed sample would cause an underestimate of the contribution of stalked species and an overestimate for non-stalked species.

Physical and chemical measurements

Conductivity measurements were made regularly. A conductiometric device utilizing an electronic bridge as described by Withrow and Withrow (1953) was used. A 1 cm^2 platinum electrode coated with black platinum was used. The calibration of the cell constant was made with standard KCl solutions. All conductivity measurements were calculated to the micromhos conductance of a standard cell at 25°C. Measurements of conductivity, total dissolved solids, and ions were made biannually by the Design and Construction Division of the Bureau of Reclamation, United States Department of the Interior (Table 1). Measurements of pH were made in the laboratory with a model "N" Beckman pH meter with standard electrodes. During warm weather water samples were refrigerated while being transported to the laboratory. In general, about 24 hours elapsed from sampling time to the time of laboratory readings. Temperatures of surface waters were measured with a calibrated thermometer. Temperatures of deeper waters were measured with a calibrated Taylor maximum-minimum thermometer.

FALLS LAKE

General description

Falls Lake (Fig. 1), referred to on some maps as Fall Lake or Dry Falls Lake, is a

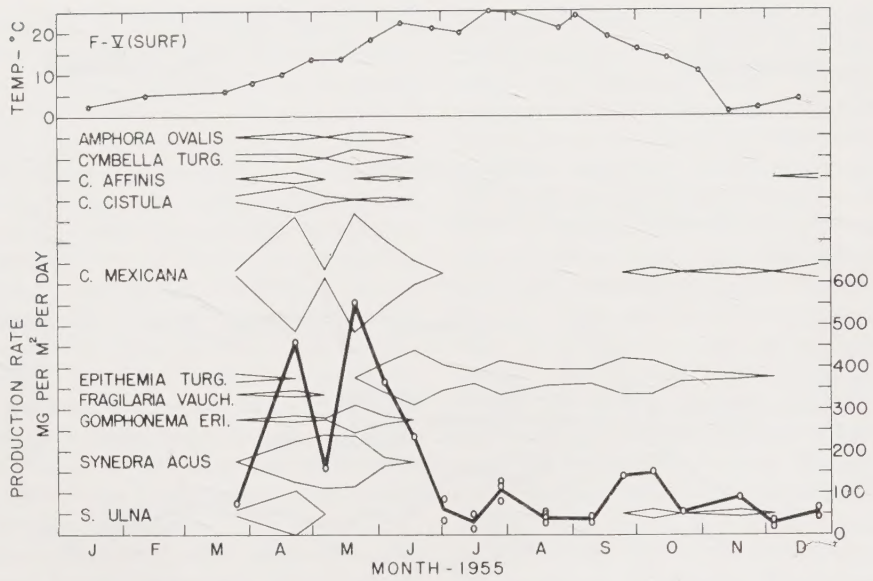

FIG. 3. Falls Lake F-V (surf) *1955*: production rate on glass as ash-free dry weight, the diatom species composition, and temperature data. No ice was present. Mid-dates of submergence periods are used.

plunge pool lake located in the westernmost alcove below Dry Falls (Sec. 6, T.24N., R.28E., Grant County). The lake has a surface area of 40.2 ha and a perimeter of 6.2 km. Indentations and promontories are numerous. Vertical basalt cliffs and steep talus slopes border about 30% of the lake; gradual slopes of predominantly inorganic sediments border about 12%; gradual slopes of organic detritus border the marshes and comprise about 58% of the total periphery. A continuous vertical wall, 90 to 125 m in height, rises above Falls Lake on the east, north, and west. The lake bottom is covered entirely with a soft brownish-grey gyttja which includes a large amount of diatomaceous material. Submerged anchored macrophytes form an open to dense cover on the bottom to a depth of about 6 m.

Nearly half of the total surface area consists of a *Typha latifolia-Scirpus validus* marsh rarely more than 1 m deep. The largest marsh area occupies the southwestern end of the lake in the gradually narrowing effluent which leads to Rainbow Lake to the south. During low water, the open water portion of the lake has a maximum depth of 10 m and an average depth of 5.4 m. The range of water level was usually about 0.3 m from high mark in March to low in September. The calculated volume of the open portion is about 1,150,000 m^3. The lake is spring-fed.

Sodium, calcium, and magnesium are the principal cations in that order of abundance (Table 1). Bicarbonate is the principal anion, with sulfate and chloride of secondary importance. The concentration of total dissolved solids ranged from 244 to 300 ppm. (Table 1). The pH of surface waters ranged from 8.0 in winter to 9.1 in late summer.

During the winters of 1954–55 and 1955–56, Falls Lake was ice covered with the exception of two narrow crescents of open water bordering the two northerly bays. These remained open apparently because of continuous subterranean inflow of warmer water and a subsequent upwelling. Surface water temperatures were as high as 7°C in these crescents through portions of both winters (Figs. 3 and 6). The lake and marsh surface froze in mid-December, 1954, and mid-November, 1955. The thaw took place in early March and late March in 1955 and 1956, respectively (Figs. 2 and 5). Ice

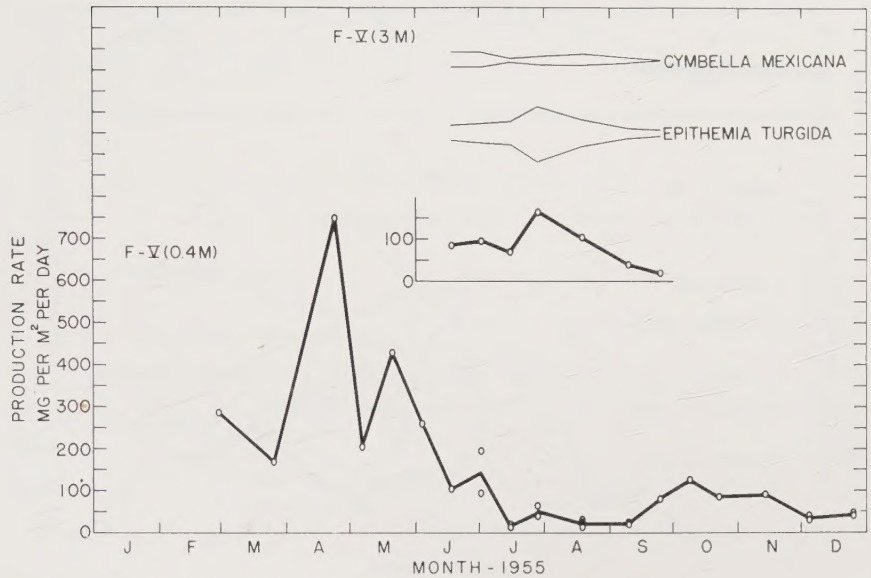

FIG. 4. Falls Lake F-V (0.4 m) and F-V (3.0 m) *1955*: production rate on glass as ash-free dry weight and the diatom species composition. Mid-dates of submergence periods are used.

thickness reached a maximum of 35 cm during January and February of 1955 and 1956. Snow, ranging from 2–10 cm in depth, covered the ice through most of both winters.

A surface water temperature of 20°C was reached or approached by late May in 1954, 1955, and 1956 (Figs. 2 and 5). Temperatures ranging from 20°C to 25°C existed until mid-September. Nearly homothermal conditions lasted until mid-May when a thermocline developed between 5 and 6 m. At this time the surface temperature was rising above 15°C, and the bottom temperature was near 9°C. Stratification generally remained until the surface temperature dropped to about 14°C in mid-October. By that time the thermocline had descended to below 6 m. During the warmest periods the bottom temperature (9–10 m) rarely exceeded 12.5°C.

Glass plate stations

Station F-I was a rocky ledge extending from 0.2 to 0.6 m depth. It was directly below a southerly facing cliff. Full light was received except during late afternoon. The station was within 15 m of the main marsh. The station was ice-covered in winter. The size of the ledge allowed the regular use of three glass plates.

Station F-V was a large gradually sloping rock at the base of a high south-westerly facing talus slope in one of the northerly bays. It was shaded during the early morning hours. The station was at least 150 m distant from the nearest marsh area. F-V was ice free during the winters. Four glass plates were generally used at a depth of 0.1 m and again at 0.4 m. Single plates were submerged at 1, 2, and 3 m depths during the summers.

Several other glass plate stations were established in other sectors of the lake. Results obtained at these stations will not be presented. A number of disturbances prevented a continuous collection of materials at these stations. Among these were destruction of plates by vandals and frequent piling up of vegetation over the plates.

Production and composition of the epilithic algae

Production rates on glass plates expressed as ash-free dry weight are shown graphically in Figures 2–7. The data from 2-week submergence periods were used except when only 4-week data were available.

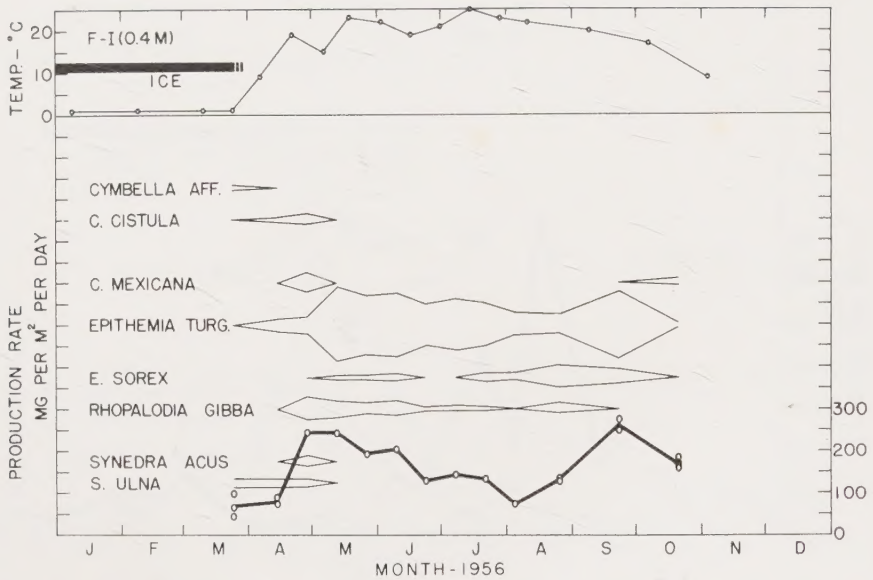

FIG. 5. Falls Lake F-I (0.4 m) *1956*: production rate on glass as ash-free dry weight, the diatom species composition, and temperature and ice data. Mid-dates of submergence periods are used.

The attachment material was composed primarily of living diatoms. The undisturbed material was examined periodically in the living state when pieces of broken glass were returned to the laboratory. Many of the common species were attached by means of gelatinous stalks (*e.g., Cymbella, Gomphonema*) while others were sessile (*e.g., Synedra, Epithemia*).

The diatom species composition on plates was similar to that occurring on the shallow rock substrate and, for that matter, on submerged macrophytes as well. In general, however, a thicker cover of diatoms was present on the permanent substrate. Permanently submerged rocks were never bare at any season. There was invariably a thin crust of blue-green algae, (*e.g., Calothrix parietina, Amphithrix janthina*) on which the attachment of diatoms and other forms took place. Only glass plates submerged for six weeks or longer showed a development of these encrusting forms. During the summer *Gongrosira* and *Entophysalis* were added to the crust.

Cladophora fracta was luxuriant on rocks and macrophytes during summer but did not occur on glass plates. The summer period was also characterized by an abundance of benthal *Oscillatoria, Phormidium,* and *Spirogyra* but these were seldom common on plates. During fall and winter *Ulothrix aequalis* was a common epilithic alga at the water-air interface but again seldom occurred on plates.

The species composition of the glass plate material was analyzed (see Materials and Methods) for stations F-I (0.4 m) and F-V (surface and 3 m) only. Those species represented graphically were dominant by volume, but many species of smaller cell size, possibly representing equal or greater division rates, could not be shown (Figs. 2–7).

Following are certain rather prominent features of plate results in Falls Lake:

1. The highest production rate generally occurred in spring or early summer.
   (a) Several species combined high production rates to form the spring pulse.
   (b) The pattern of occurrence of spring species was rather similar in 1955 and 1956.
   (c) Total production rate was lower in the spring of 1956.
2. The lowest production rate generally occurred in late summer.

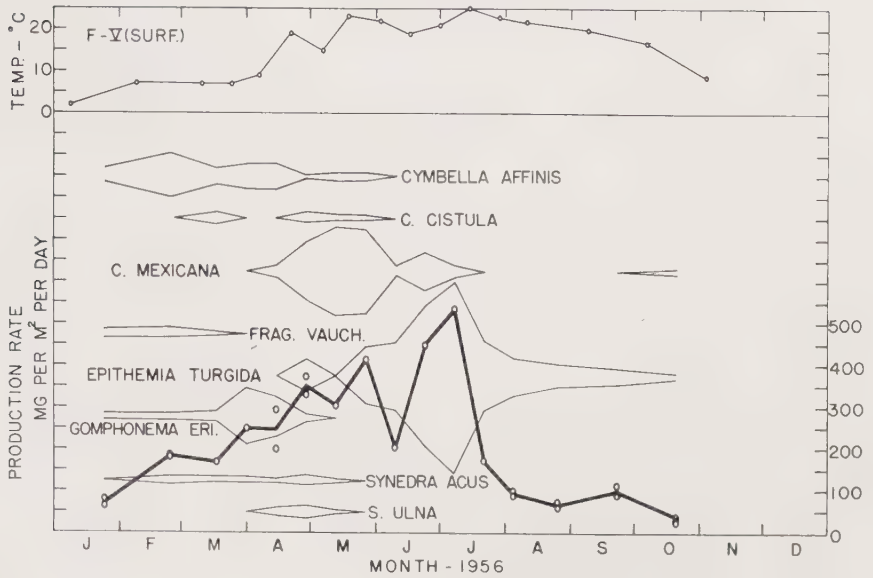

FIG 6. Falls Lake F-V (surf) *1956*: production rate on glass as ash-free dry weight, the diatom species composition, and temperature data. No ice was present. Mid-dates of submergence periods are used.

(a) Only a few species showed greatest production in the summers.
(b) The dominant species of spring and summer were usually not the same.
(c) A few of the spring dominants remained abundant through the summer at lower depths.

3. A second but generally smaller pulse occurred in the fall. The fall pulse was composed of summer dominants plus a few of the spring dominants.
4. The production rate was fairly low in winter, particularly under ice and snow cover.

1955. Highest production rates were obtained at all stations in April (Figs. 2–4), although high production was evident as early as February at F-V (Fig. 4), which was ice-free. Production under the ice and snow apparently made a steady ascent from an extremely low rate in January to the pulse in April, which occurred soon after the thaw (Fig. 2). *Acnanthes minutissima* var. *cryptocephala, Cymbella affinis, C. cistula, C. mexicana, Fragilaria vaucheriae, Gomphonema eriense, Synedra acus,* and *S. ulna* were the commonest winter diatoms (Fig. 2). Very little qualitative difference existed between the ice-covered and ice-free areas.

The spring pulse was in effect a period of increasing production rates for *Amphora ovalis, Cymbella affinis, C. cistula, C. mexicana, C. turgida, Fragilaria vaucheriae, Gomphonema eriense, Synedra acus,* and *S. ulna* (Figs. 2 and 3). An increase in abundance was also observed in *Acnanthes minutissima, Cocconeis placentula, Cymbella ventricosa, Fragilaria brevistriata, Nitzschia amphibia, N. dissipata, N. frustulum, N. gracilis, N. linearis, N. palea,* and *Synedra rumpens.*

At F-V there was a prominent second maximum in May. This was primarily dominated by *Synedra acus, Cymbella mexicana,* and *Gomphonema eriense* (Fig. 3). Although a second spring pulse was not exhibited at F-I the decline that followed the first peak was, nevertheless, a maximal period for *Synedra acus* (Fig. 2). This species was conspicuously dominant on all plates and rocks during this period and in the plankton as well.

The spring diatom communities formed thick greyish-brown to yellowish-brown

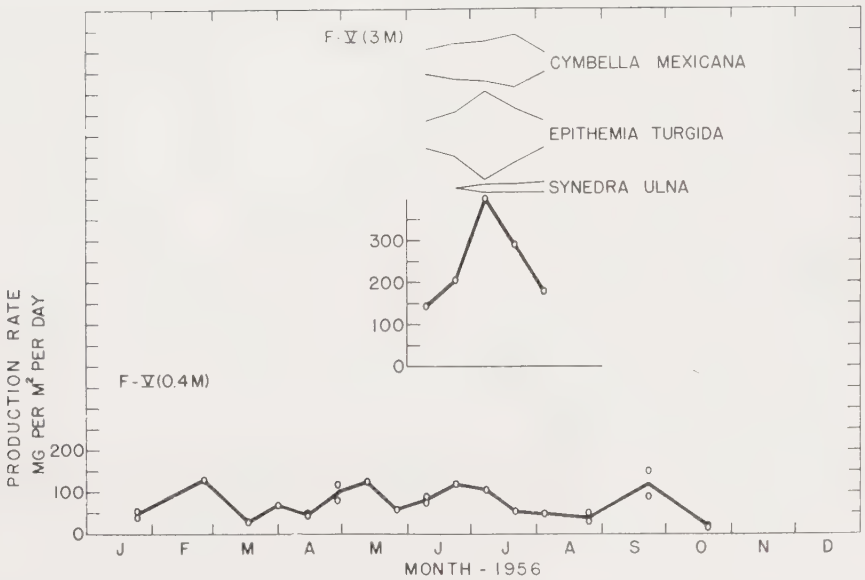

FIG. 7. Falls Lake F-V (0.4 m) and F-V (3.0 m) *1956*: production rate on glass as ash-free dry weight and the diatom species composition. Mid-dates of submergence periods are used.

coatings on rocks and plates. The coating on rocks often reached a thickness of over 1 cm. There was a gradual lessening of the diatom cover with increasing depth, at least below 1 m. Species of *Cymbella* at first formed distinct tufts, but when growth of this genus and others became widespread the tufts were consolidated into a continuous mat. By mid-April the mat had reached such a thickness that gas became trapped and sections or fragments would consequently rise to the surface. On some days the entire surface of the lake would be charged with clots of detached diatoms.

By early or mid-June there was a general decline in production rate at both stations. A minimum was reached in August in all cases (Figs. 2–4). It should be noted, however, that summer was the period of greatest abundance of *Epithemia turgida* (Figs. 2–4). This was also true for *Epithemia sorex* and *Rhopalodia gibba*. The summer diatoms formed a thin, tightly-held crust on rocks and glass plates. *Acnanthes minutissima, Cocconeis pediculus, C. placentula,* and *Fragilaria brevistriata* were also common.

The highest production rate during midsummer occurred at 3 m-depth at F-V (Fig. 4). Slightly lower but similar curves were produced at 2 m and 1 m. The results at 3 m are interesting in that *Cymbella mexicana* was abundant at that depth on both glass and rocks, while it had been reduced to rarity in water shallower than about 1.5 m. *Cymbella cistula* and *Synedra ulna* followed the same pattern to some extent.

A small increase in production rate was evident at F-V (and possibly at F-I) during September and October (Figs. 2–4). This was primarily a result of a continued abundance of *Epithemia turgida*, but it may also be seen that *Cymbella mexicana* and *Synedra ulna* had returned in some abundance in shallow water by late October (Figs. 2 and 3). Other common diatoms of the fall were *Acnanthes minutissima, Amphora ovalis, Cocconeis placentula, Cymbella affinis, C. cistula, C. turgida, C. ventricosa, Epithemia sorex, Gomphonema parvulum,* and *Synedra acus.*

There was a visible change in the appearance of the diatom coating on rocks during this period. The crusty summer coating consisting mainly of *Epithemia* became a softer yellowish-brown mat similar in appearance to that of early spring but of less thickness.

The late fall period was attended by a gradual decline in production rate with

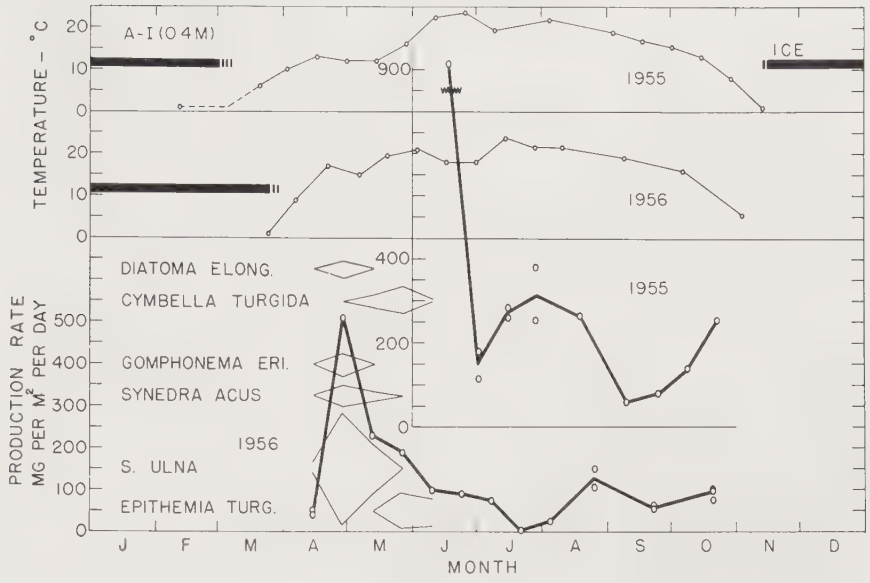

FIG. 8. Alkali Lake A-I (0.4 m) *1955* and *1956*: production rate on glass as ash-free dry weight, the diatom species composition, and temperature and ice data. Mid-dates of submergence periods are used.

minimum values attained in December (Figs. 2–4). The decline was a reflection of the decreased abundance of most species with the exception of *Cymbella affinis* and *C. mexicana* (Fig. 3).

1956. The spring production rates of 1956 were generally lower than those of 1955 (Figs. 5–7). A spring pulse was evident at F-I (0.4 m) and F-V (surface) but was conspicuously absent at F-V (0.4 m) (Fig. 7). This seems incongruous with results obtained in 1955 when the surface and 0.4 m-depths exhibited values and curves that were quite similar (Figs. 3 and 4). Both F-I and F-V 0.4 m-stations of 1956 were similar in that spring values were low relative to values at the surface station. At the surface station increasing production was evident as early as February, and there was a continuous increase until late May at which time the spring pulse ended (Fig. 6). It should be remembered that station F-V was ice-free and with higher temperatures in February and March (Fig. 6). The species composition on the plates and on the shallow rocks at F-V was comparable to that of 1955. However, *Cymbella affinis* and *Gomphonema eriense* peaks appear to have been earlier in 1956, and *Synedra acus* and *S. ulna* peaks were not so well developed (Fig. 6).

An examination of the species composition at F-I leads to a partial explanation of the relatively low production rate in spring. A very low production rate was recorded under the ice and snow cover. After the late thaw there was only a short flourish of spring species which were soon replaced by the summer dominants, namely *Epithemia turgida, E. sorex,* and *Rhopolodia gibba* (Fig. 5). During the spring pulse *Cymbella mexicana* and *Gomphonema eriense* never reached any sizable proportions (Fig. 5). This statement also applies to the 0.4 m-depth at F-V although the species composition was not completely analyzed.

A conspicuous feature of summer production at the surface at F-V was the very heavy growth of *Epithemia turgida* during late June and July (Fig. 6). This was true to a lesser extent at F-I (0.4 m) where mid-summer production by *E. turgida* was only a little less than production in May (Fig. 5). At F-V (0.4 m) summer production figures were quite low, although this was an inexplicable feature at this station through all the seasons (Fig. 7). At 3 m- and 2m-depths, however, mid-summer production

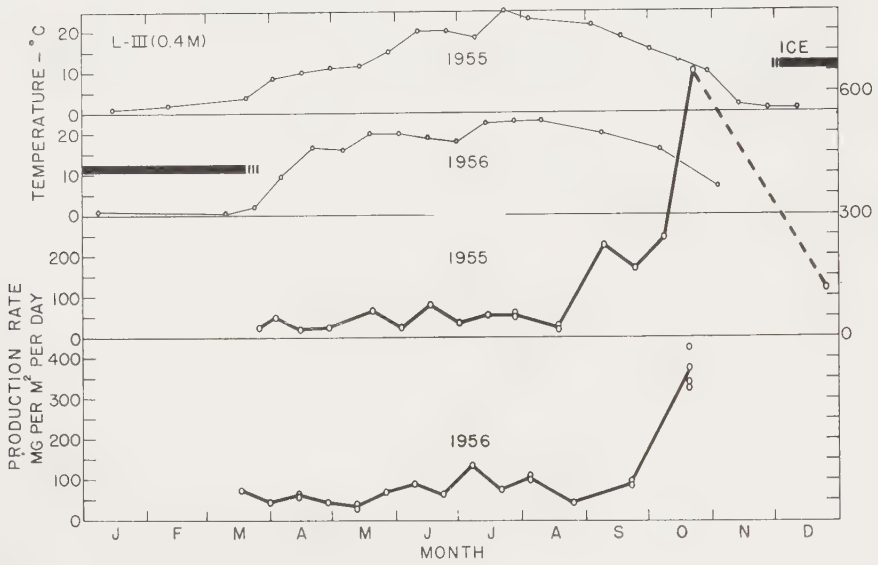

FIG. 9. Lake Lenore L-III (0.4 m) *1955* and *1956*: production rate on glass as ash-free dry weight and temperature and ice data. Mid-dates of submergence periods are used.

was even higher than in 1955, and, as before, the characteristic spring species *Cymbella mexicana* and *Synedra ulna* were quite common (Fig. 7).

At all stations a summer minimum was reached in August which agrees with the results of 1955. A rise in production rate in September was significant only at F-I (0.4 m). The characteristic summer species were again dominant (Fig. 5). However, as in 1955, several spring species reappeared at all stations by October. At about this time there was a general decline in production at all stations (Figs. 5–7).

With the various exceptions noted, the seasonal distribution of species followed the same general pattern as in 1955.

ALKALI LAKE

General description

Alkali Lake, located about 11 km southwest of Falls Lake (Fig. 1), is the southernmost lake of the freshwater chain. The major portion of the lake is located in Sec. 31, T.24N., R.27E., Grant County. The lake has a surface area of approximately 95 ha and a perimeter of 7.3 km. A large part of the perimeter consists of gently sloping shores of compact inorganic sediments. A smaller part consists of fairly steep talus and vertical basalt cliffs. The canyon wall close to the southeasterly shore rises to 150 m above the lake surface. It is a shallow lake with a maximum depth of about 4 m and an average depth of about 2 m. The large southernmost bay is very shallow, rarely over 1 m in depth. No marshes have yet developed in Alkali Lake. The entire lake basin, however, is covered by submerged anchored macrophytes. The benthal substrate is a soft dark gyttja.

The lake was originally a part of Lake Lenore to the south and was isolated by the road fill of the present highway about 1936. Lake Lenore was then and remains a saline lake. The total dissolved solid content of Alkali Lake ranged from 356 to 440 ppm (Table 1). A freshwater influent passes from Blue Lake to Alkali Lake. The effluent from Alkali Lake to Lake Lenore consists of a flow through the coarse rocks of the road fill during high water. Sodium and magnesium are the principal cations, while bicarbonate is the dominant anion (Table 1). The pH of Alkali Lake surface waters ranged from 8.4 in the colder months to 9.4 in late summer.

The lake became ice and snow covered in mid-December 1954, and mid-November

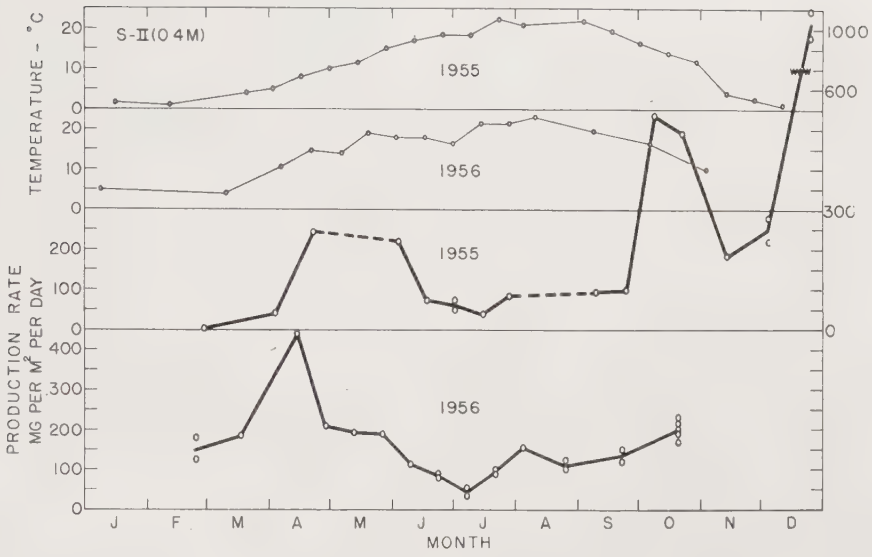

FIG. 10. Soap Lake S-II (0.4 m) *1955* and *1956*: production rate on glass as ash-free dry weight and temperature data. No ice was present. Mid-dates of submergence periods are used.

1955. The thaw occurred in early March 1955, and late March 1956 (Fig. 8). The annual temperature curves of surface waters were similar to those of Falls Lake (Fig. 8). Essentially homothermal conditions existed throughout the year in Alkali Lake.

The water level fluctuated greatly. In the spring of 1955 the level fell about 1.5 m. The water was lost through the road fill into Lake Lenore, which had been lowered artificially. The rapid water drop in Alkali Lake caused a great amount of turbidity and sedimentation throughout the spring period. In 1956 the spring level dropped gradually 1.0 m by fall; retention dikes had been constructed.

Glass plate stations

Station A-I (0.4 m) was located off a gradually sloping rocky point in the southeastern corner of the main (northern) section of the lake. Rubber cups were used on the plates because of the rough nature of the bottom rock. The station was not shaded during any part of the day. The rock shelf of the station was located within a few meters of dense *Myriophyllum-Potamogeton* beds. Three plates were generally used.

A few other glass plate stations were used temporarily during the spring and early summer of 1955. Because of heavy sedimentation and continuous breakage only scattered results were obtained.

Production and composition of the epilithic algae

Production rates on glass plates are shown in Figure 8. The species composition was not completely analyzed as in Falls Lake. The glass plate attachment material was composed of a large percentage of green algae together with diatoms except for brief almost pure diatom blooms in spring. Thus, except for this short period it was impossible to plot diatom volumes as percentages of the total ash-free dry weight.

In general the attachment material on glass plates was quite similar to that on the rock substrate. Exceptions were the great abundance of the epiphytic *Gloeotrichia pisum* on the lower surface of plants during summer and the absence of some epilithic green algae on plates (*i.e.*, *Ulothrix aequalis* and *Cladophora fracta*).

At the time of the thaw in 1955 and 1956 (Fig. 8) a brief bloom composed mainly of *Fragilaria vaucheriae* and *Synedra acus* formed a thin brownish coating on rocks and vascular plants.

A large spring diatom pulse occurred in

early May 1955, and late April 1956. In both years the pulse was initiated after surface water temperature had risen to about 13°C. Because of particularly heavy sedimentation and frequent breakage of glass plates in the spring of 1955 the recording of quantitative data at A-I (0.4 m) began in June. In 1955 the pulse was composed primarily of *Diatoma elongatum, D. vulgare, Fragilaria vaucheriae, Gomphonema eriense, G. olivaceum, Rhoicosphenia curvata,* and the green alga *Stigeoclonium* sp. In 1956 the main species were as follows: *Cymbella cistula, Diatoma elongatum, D. vulgare, Fragilaria vaucheriae, Gomphonema eriense, G. olivaceum, Nitzschia dissipata, N. gracilis, Synedra acus, Synedra ulna,* and *Stigeoclonium* sp. Other common though not abundant spring diatoms in 1955 and 1956 were *Acnanthes minutissima, Amphora ovalis, Cymbella mexicana, C. turgida, C. ventricosa, Nitzschia amphibia, N. angustata, N. frustulum,* and *N. linearis.*

At the peak of spring production plates and rocks were covered with satiny yellowish-brown diatom tufts usually consolidated into a continuous mat, which was nearly 1 cm thick in 1956. Bright green tufts of *Stigeoclonium* were dispersed through the diatom mat. Below 1 m there was a striking reduction in the amount of diatom cover. Shallow macrophytes were also covered by heavy coatings of the same diatoms. However, by early or late June plates and other substrates appeared almost bare, and production had decreased considerably.

In 1955 extremely high production values were obtained early in June. This was due primarily to a heavy growth of *Epithemia turgida, E. sorex, Cymbella turgida, C. ventricosa,* and *Scenedesmus* spp. The production rate during the remainder of the summer was fairly high with a minimum reached in September. Dominant plate and epilithic algae throughout the summer were those mentioned above plus *Closterium* sp., *Cosmarium* spp., *Tetraedron minimum,* and *Cocconeis placentula.* Shaded surfaces of rock were well covered with a nodular green crust of *Gongrosira* sp. Most rocks in Alkali Lake had a crust of blue-green algae thinner but similar to that in Falls Lake. *Amphithrix janthina* and *Calothrix parietina* were present.

In 1956 the decline in production continued from late May to early August. The species composition was, nevertheless, similar to that of the previous summer. The diatoms *Cymbella turgida, C. ventricosa, Epithemia sorex,* and *E. turgida* dominated the glass plate material until mid-June when the various green algae became more abundant.

During summer months macrophytes were covered by spherical colonies of *Gloeotrichia pisum.* The heaviest infestation occurred in August or September of 1954, 1955, and 1956. The undersides of glass plates also showed an abundance of this alga, but it was rare on the topsides and on rocks.

A distinct fall production peak was realized in October 1955, when water temperature had dropped to 15°C. A fall increase comparable to that of 1955 was not evident in 1956. Most of the important diatoms and green algae of summer remained plentiful through the fall. Conspicuous in that respect were *Closterium* sp., *Scenedesmus* spp., *Tetraedron minimum, Cocconeis placentula, Cymbella turgida, C. ventricosa,* and *Epithemia sorex. Amphora ovalis, Cymbella cistula, Fragilaria vaucheriae, Nitzschia amphibia, N. dissipata, Synedra acus,* and *S. ulna* were common spring diatoms that returned in some abundance at least during one fall period.

The great thickness of ice on Alkali Lake prevented much sampling during midwinter. The curve in Figure 8 would suggest that production was very low during that period.

LAKE LENORE

General description

Lake Lenore, located immediately south of Alkali Lake, is the largest of the Lower Grand Coulee lakes and is saline (Fig. 1). It falls primarily in Sections 11, 12, 14, 23, 24, and 35, T.23N., R.26E., Grant County. The surface area is about 556 ha, the length is 9.2 km, and the maximum width is 0.9 km. The perimeter is 21.5 km.

A large part of the periphery is intersected by steep bedrock and talus slopes from the western wall of the canyon. The eastern side possesses a great proportion of gradually sloping shores which consist of predominantly mineral sediments and boulders. The high water mark of the latter type of shoreline is marked by a belt of *Distichlis stricta* and *Scirpus nevadensis*. No submerged macrophytes were found in Lake Lenore with the exception of a few patches of *Potamogeton pectinatus* near the seepage from Alkali Lake at the northern end.

The maximum depth is 11 m, and the mean depth 6.5 m (Anderson 1958). Lake Lenore occupies a long narrow trough which is divided into basins. The bottom is mostly rocky, but extensive areas are composed of gyttja. The calculated water volume in 1950–51 was 36,042,000 m^3 (Anderson 1958). The lake is holomictic and stratified only temporarily in late spring. During the summer and winter homothermal conditions existed. In the winter of 1954–55 the northern and southern ends of Lake Lenore were ice-covered from early January to early March. The main glass plate station was entirely ice-free. In the following winter the entire lake had an ice and snow cover from early December to late March (Fig. 9). The temperature curves of surface water were similar to those of Alkali Lake and Falls Lake (Fig. 9).

The concentration of total dissolved solids ranged from 7,500 to 11,040 ppm during the course of the study (Table 1). The predominant ions were sodium, carbonate, sulfate, and chloride (Table 1). The pH ranged from 9.5 to 9.7. A more detailed account of chemical and physical variables is to be found in Anderson (1958). During Anderson's study, phosphate was high in early spring (195μg/L), fluctuated through the summer and remained at about 20μg/L during the rest of the year.

Since the beginning of this study there has been a considerable lowering of the water level by means of pumps to alleviate the problem of a rising water table. Consequently there was a heavy inflow of freshwater from Alkali Lake through the separating road fill. This occurred mainly during the high water period of late winter and spring. The result was a considerable freshening of the northern reaches of Lake Lenore in 1955. The conductivity of northern water was reduced from about 12,000 micromhos to values as low as 1,000 micromhos a few hundred meters away from the road fill. Values varying from 4,000 to 9,000 micromhos existed in the northern waters throughout the summer after the seepage had been reduced considerably. Freshwater seepage was reduced in 1956, and the conductivity of northern waters not immediately adjacent to the road fill was seldom lower than 10,000 micromhos.

Glass plate stations

The main station, L-III (0.4 m), was located midway on the east shore. The littoral region is gradually sloping and consists of fine and coarse sediments with scattered boulders. A tripod mount was used on the three plates. The plates were unshaded throughout the day. Stations L-I and L-II were located in the northern bays near the road fills. Generally qualitative data only were obtained from these plates since heavy sedimentation occurred through most of the year.

Production and composition of the epilithic algae

The epilithic vegetation of Lake Lenore may be divided into the following three types: (1) the slowly growing green crust of *Gongrosira* sp. which was tightly adhesive to rocks and most prominent on shaded sides, (2) the perennial tough coating of blue-green algae, primarily *Calothrix parietina, Amphithrix janthina,* and *Plectonema nostocorum,* and (3) the rapidly growing yellowish-brown film of diatoms. The diatom film covered the "bare" rocks and the other algal rock coatings during most of the year, and it was the dominant algal assemblage on glass plates.

Diatoms frustules were weakly silicified in Lake Lenore and were greatly deformed during ashing. The ash developed a glazed crust, and uniform suspensions and counts could not be made (see below).

The curves of production rates of ash-

free material at station L-III (0.4 m) were quite similar in 1955 and 1956 (Fig. 9). Production rates were low in the spring and summer until September. *Nitzschia frustulum* var. *minutula* Grun., *N. frustulum* var. *tenella* Grun., and *N. palea* var. *Kuetzingiana* Hilse were essentially the sole dominants during early spring (March and April), while *Amphora salina* W. Sm. (var.) and, to a lesser extent, *Amphora coffeaeformis* (Ag.) Kuetz. (var.) were also very important in May. The species of these two genera continued as dominants through the summer period, but *Anacystis marina* (Hansg.) Dr. & Daily, *Plectonema nostocorum, Oőcystis* sp., and *Gloeocystis* sp. were occasionally important on plates. During the entire summer of 1956 *Stigeoclonium* sp. was one of the dominant algae on plates, particularly on the underside.

Stigeoclonium first became established in Lake Lenore in May of 1955 following the first significant freshening of northern bays. It appeared only on rocks and plates adjacent to the Alkali Lake road fills. It was common at this time in Alkali Lake. Soon it spread to nearly all shores of the north end of Lake Lenore. It remained abundant in this area through the summer and fall. In late spring of 1956, it reappeared, first in the north end as before, but by June it occupied the littoral regions of the entire lake. According to G. C. Anderson (personal communication) it was not observed in Lake Lenore before 1955.

A steep increase in production occurred in September or October of both years (Fig. 9). A high rate continued in the fall of 1955 probably until the time of ice formation. One winter reading gave a relatively low rate during late December. *Nitzschia* spp. and *Amphora* spp. were the dominant elements of the fall pulse, although *Anacystis marina, Stigeoclonium,* and *Gloeocystis* were also important in 1956. During these periods of high production rocks of the shallow littoral became covered with soft yellowish-brown diatom mats which often loosened and peeled.

The high diatom production corresponded approximately to periods of cooler temperatures (15°–5°C) and of low light intensity and duration. Anderson described phytoplankton volume and chlorophyll content curves which were somewhat similar to the attached algal production curves of the present study, although he found a distinct spring pulse as well as one in the fall. The spring phytoplankton pulse consisted primarily of *Amphora* sp. (almost certainly *A. salina* var.), while *Chaetoceros elmorei* dominated the fall pulse.

Besides the rather distinctive assemblages of epilithic algae, there was a conspicuous loose and continuously shifting benthoplankton composed of blue-green algae in the form of crumbly gelatinous aggregates. The primary constituents were *Anacystis marina* and *Plectonema nostocorum.* The benthal algae which covered a major part of the basin of Lake Lenore are described more extensively by Castenholz (1957).

SOAP LAKE

General description

Soap Lake, the southernmost of the Grand Coulee lakes, is also the most saline. It is located in Sections 12, 13, and 24, T.22N., R.26E., and Sections 18 and 19, T.22N., R.27E., Grant County (Fig. 1). The surface area is about 360 ha. The length is 3.6 km and the maximum width is 1.3 km. The perimeter is about 10 km. The shape is more or less rectangular and quite regular. The major portion is bordered by bedrock intersecting the water at a rather gradual angle. Much of the southern and northern ends consists of gradually sloping mineral sediments. In certain areas there is a shallow shelf-like crust of precipitated carbonates. As in Lake Lenore, part of the shoreline is bordered by a narrow belt of *Distichlis stricta* and *Scirpus nevadensis.* There are no submerged macrophytes.

The maximum depth is about 27 m and the mean depth is about 10 m. Black organic deposits cover most of the lake bottom. The lake is meromictic. Summer thermal stratification occurs in the mixolimnion. The chemocline was found below 14 m (Anderson 1958). The calculated volume is about 36,500,000 m^3.

The water is capable of forming a froth and is generally quite clear. There is no

surface influent or effluent, although a subterranean inflow from Lake Lenore has been suggested (Anderson 1958). The concentration of total dissolved solids in surface waters ranged from 25,440 ppm in 1954 to 20,600 ppm in 1956 (Table 1). According to Anderson the maximum concentration in the monimolimnion has remained at about 144,000 ppm. There has been over a 40% reduction in salinity of surface waters since 1949 at which time 35,000 ppm was an average value (Anderson 1958). The predominant ions were sodium, carbonate, sulfate, and chloride as in Lake Lenore (Table 1). The pH ranged from 9.5 to 9.8. A more complete discussion of physical-chemical properties of Soap Lake is to be found in Anderson (1958).

During the winter of 1954–55 Soap Lake was completely ice-free (the freezing point of surface was about –1.4°C). During the following winter ice and snow covered most of the lake from January to mid-March. The peripheral waters, including the site of the plate station, were generally open however. The temperature curves of surface water show a relatively slow warming in spring and a slow cooling in fall (Fig. 10).

Glass plate stations

Several stations were used at various times in Soap Lake. Breakage of plates was so frequent, however, that ultimately only one station was maintained through the course of the study. Breakage was due not only to vandalism but also to the frequently heavy wave action. High winds were most comcon in winter and spring. Stations S-II (0.4 m) was located in the northeastern corner of the lake and was fairly well protected from heavy wave action by a few small promontories to the south. The littoral region is a gradually sloping shelf rock with coarse gravel and some small boulders. The shelf drops off rather suddenly to 5 m depth about 14 m from shore. Three plates mounted on a tripod were generally used. S-II was ice-free through the entire course of study.

Production and composition of the epilithic algae

The flora of Soap Lake was fairly similar to that of Lake Lenore. The epilithic diatom assemblages were quite similar. *Gongrosira* formed an epilithic crust in both lakes. A characteristic "crumbly" type of benthoplankton composed of blue-green algae covered much of the bottom in both lakes, but a prominent thick epilithic coating of blue-green algae was absent in Soap Lake.

As in Lake Lenore several difficulties prevented an analysis of the species composition on glass plates (see below).

Production rate curves in 1955 and 1956 were similar (Fig. 10). The same was true in Lake Lenore. Production increased greatly in fall, but unlike the situation in Lake Lenore a large winter and spring pulse was evident in Soap Lake (Fig. 10). The principal glass plate constituents were the diatoms *Nitzschia frustulum* var. *minutula*, *N. frustulum* var. *tenella*, *N. palea* var. *kuetzingiana*, *Amphora salina* var., and the blue-green alga *Anacystis marina*. These taxa were dominant during blooms and during low production as well. However, for a few weeks in June 1955 and May 1956 *Oőcystis* sp. was also a dominant. *Plectonema nostocorum* was common on plates throughout the summer. The high production of fall and winter in 1955 consisted predominantly of the diatoms mentioned above, although *Chlamydomonas* sp. was important on plates and as inshore plankton. The extremely high winter rate observed in December 1955 in Soap Lake, when compared to the low rate at the same time in Lake Lenore, may be explained by the presence of an ice and snow cover over the station in Lake Lenore at that time (Fig. 9). The study was not followed through late fall and winter of 1956, but the production curve showed a steady ascent through late October (Fig. 10).

Anderson (1958) studied the phytoplankton of Soap Lake in 1950 and 1951. Although he did not determine the volume of phytoplankton, his curves representing chlorophyll content of the water in the mixolimnion correspond well with the production rate curves of attached algae in the present study. *Amphora* sp. (presumably *A. salina* var.) was the dominant phytoplankter during Anderson's study. The explanation proposed by Anderson for the low chlorophyll content in summer was that

phytoplankton was reduced mainly by extensive zooplankton grazing. Using suspended bottles he demonstrated that grazing was effective in reducing the size of the phytoplankton population in Soap Lake. Using the same technique he was unable to demonstrate the same effect with regard to organisms in Lake Lenore. It was suggested (Anderson *et al.* 1955) that production rate remained high during the periods of chlorophyll decline. The epilithic and plate diatoms, including a large proportion of *Amphora salina*, were not significantly affected by zooplankton grazing. The cladoceran and rotifer zooplankters of Soap Lake were most abundant in open water; concentrations along the shore seldom occurred. Insect larvae, although sometimes common, never appeared abundant enough during late spring and summer to influence the apparent low production values. It is suggested, then, that the decline in production rate was real as far as the epilithic diatoms are concerned. Probably there was a real decline in production rate of the phytoplankton as well, since *Amphora* was common to both situations, and it is likely that the same factors would apply. It should be remembered, however, that the two studies were not carried on concurrently.

A FLORISTIC COMPARISON

The lakes of the Lower Grand Coulee fall easily into two classes—freshwater and saline. Alcove Lake (Fig. 1) is the only body of water approaching intermediate conditions. During high water salinities as low as 3,000 ppm T.D.S. were reached; salinities rose as high as 8,000 ppm T.D.S. during low water. It was not surprising to find both characteristic freshwater and saline species of algae in Alcove Lake together with several taxa seemingly restricted to this lake.

The truly freshwater lakes of the Lower Grand Coulee were found to have about 234 species and varieties compared to 65 for the saline lakes (including Alcove and Talus Lakes). In both classes of lakes diatoms and blue-green algae were well represented in numbers of species; green algae were well represented in the freshwater lakes only

TABLE 3. *The number of taxa occurring in four lakes of the Lower Grand Coulee*

Class	Falls	Alkali	Lenore	Soap
Chlorophyceae	74	45	8	7
Charophyceae	1	1	0	0
Euglenophyceae	2	1	2	1
Xanthophyceae	9	0	0	1
Chrysophyceae	3	1	0	0
Bacillariophyceae	86	70	15	11
Dinophyceae	4	1	0	0
Cryptophyceae	1	0	0	0
Cyanophyceae	39	17	12	10
Total	219	136	37	30

(Table 3). There were 25 algal taxa common to freshwater and constantly saline lakes (Lenore and Soap). These include, *Botryococcus braunii, Gongrosira* sp., *Stigeoclonium* sp., *Anomoeoneis sphaerophora, Campylodiscus clypeus, Nitzschia frustulum, Amphithrix janthina, Anacystis marina, Calothrix parietina, Plectonema nostocorum,* and others. All of the blue-green algae mentioned play dominant roles in the saline lakes and occasionally in freshwater lakes as well. *Stigeoclonium* and *Gongrosira* were important in both classes of lakes. *Nitzschia frustulum* was an abundant epilithic and glass plate diatom in the saline lakes only. Since no single taxon represents a dominant attachment form on glass in both classes of lakes, no comparison of specific production rates in the two habitats could be made. It should also be borne in mind that the taxa shared by both classes of lakes may not be the same genetically.

Although Falls Lake and Alkali Lake are both freshwater a sizeable floristic difference existed between the two (Table 3). Falls and Alkali Lakes shared about 106 taxa. Falls Lake, however, had 105 taxa not found in Alkali Lake. Many of these were species restricted to the marsh habitat. Twenty-three taxa found in Alkali Lake were not collected in Falls Lake, but almost all occurred in other freshwater lakes in the area. It is impossible with the information at hand to speculate on factors influencing the floristic differences and similarities between these two lakes. They are similar in gross chemistry (Table 1) although Alkali

TABLE 4. *Ash-free dry weight of attached materials from* freshwater lakes *expressed as milligrams per square meter per day and as percentage of total dry weight; two week results are in roman type, four week results are in italics; mid-dates of submergence periods are used*

Date 1955	Stations									
	F-I (0.4m)		F-V (surf.)		F-V (0.4m)		F-V (3m)		A-I (0.4m)	
	mg	%	mg	%	mg	%	mg	%	mg	%
1-1	*72*	*43*	–	–	–	–	–	–	–	–
1-27	*45*	*48*	–	–	–	–	–	–	–	–
2-28	*287*	*38*	–	–	*284*	*41*	–	–	–	–
3-12	200	40	–	–	–	–	–	–	–	–
3-25	248	35	75	52	171	38	–	–	–	–
4-2	*603*	*38*	–	–	–	–	–	–	–	–
4-8	452	33	–	–	–	–	–	–	–	–
4-15	*856*	*40*	–	–	–	–	–	–	–	–
4-22	535	40	458	40	748	43	–	–	–	–
4-29	*403*	*35*	*211*	*29*	*381*	*36*	–	–	–	–
5-6	171	32	161	20	204	38	–	–	–	–
5-13	*144*	*36*	*250*	*31*	*513*	*38*	–	–	–	–
5-20	123	37	554	30	428	41	–	–	–	–
5-27	*95*	*31*	*575*	*33*	*231*	*38*	–	–	–	–
6-3	149	33	363	44	259	44	–	–	–	–
6-10	*153*	*34*	*357*	*31*	–	–	–	–	–	–
6-17	159	33	233	33	103	42	84	43	916	21
6-24	*99*	*40*	*151*	*29*	*89*	*38*	–	–	–	–
7-1	100	43	36	36	96	42	94	34	116	39
7-1	–	–	85	33	197	64	–	–	181	37
7-8	*35*	*37*	*46*	*30*	*36*	*36*	–	–	–	–
7-15	31	41	16	30	13	37	71	38	259	43
7-15	–	–	51	24	19	36	–	–	286	46
7-21	*67*	*32*	*127*	*18*	*84*	*29*	–	–	*318*	*37*
7-28	56	29	81	28	38	35	167	48	253	47
7-28	–	–	118	17	42	33	–	–	380	46
7-28	–	–	126	20	64	39	–	–	–	–
8-7	*35*	*30*	–	–	–	–	–	–	–	–
8-13	25	30	–	–	–	–	–	–	–	–
8-18	*26*	*34*	*30*	*33*	*16*	*26*	*105*	*43*	*266*	*37*
8-18	–	–	*39*	*35*	*21*	*34*	–	–	–	–
8-18	–	–	*44*	*26*	*27*	*38*	–	–	–	–
8-18	–	–	*52*	*20*	*32*	*36*	–	–	–	–
8-28	29	33	–	–	–	–	–	–	–	–
9-4	*49*	*39*	–	–	–	–	–	–	–	–
9-9	53	41	30	25	22	41	39	40	59	42
9-9	–	–	45	22	24	34	–	–	–	–
9-17	*47*	*38*	*127*	*18*	*65*	*41*	–	–	*108*	*44*
9-17	–	–	*131*	*28*	*80*	*30*	–	–	–	–
9-24	51	40	139	18	80	36	22	46	81	49
10-1	*93*	*42*	*126*	*25*	*83*	*44*	–	–	–	–
10-8	61	40	151	35	133	50	–	–	139	51
10-15	*78*	*35*	*110*	*21*	–	–	–	–	*158*	*41*
10-15	–	–	*113*	*25*	–	–	–	–	–	–
10-22	74	31	53	22	86	33	–	–	253	40
11-13	*26*	*27*	*89*	*19*	*88*	*24*	–	–	–	–
11-13	*35*	*30*	–	–	–	–	–	–	–	–
12-4	4	14	20	41	30	30	–	–	–	–
12-4	11	50	35	43	42	32	–	–	–	–
12-25	–	–	*47*	*36*	*39*	*37*	–	–	–	–
12-25	–	–	*65*	*39*	*46*	*40*	–	–	–	–

Date 1956	Stations									
	F-I (0.4m)		F-V (surf.)		F-V (0.4m)		F-V (3m)		A-I (0.4m)	
	mg	%	mg	%	mg	%	mg	%	mg	%
1-24	–	–	*67*	*34*	*41*	*41*	–	–	–	–
1-24	–	–	*83*	*38*	*54*	*36*	–	–	–	–
2-24	–	–	*186*	*35*	*131*	*38*	–	–	–	–
2-24	–	–	*187*	*35*	–	–	–	–	–	–
3-17	–	–	172	13	30	20	–	–	–	–
3-24	*47*	*27*	*203*	*16*	*30*	*23*	–	–	–	–
3-24	*64*	*29*	–	–	*60*	*20*	–	–	–	–
3-24	*101*	*31*	–	–	–	–	–	–	–	–
3-31	–	–	252	13	69	22	–	–	–	–
4-7	–	–	*301*	*22*	*31*	*36*	–	–	–	–
4-14	76	28	199	21	43	39	–	–	38	9
4-14	88	32	296	20	50	29	–	–	52	10
4-21	*275*	*29*	*354*	*22*	*138*	*35*	–	–	*585*	*23*
4-28	243	27	329	20	81	32	–	–	508	33
4-28	–	–	373	18	119	25	–	–	–	–
5-5	*186*	*30*	–	–	–	–	–	–	*322*	*26*
5-12	245	33	307	22	125	31	–	–	232	25
5-19	*173*	*30*	–	–	–	–	–	–	*78*	*17*
5-26	196	27	416	22	61	30	–	–	192	15
6-2	*245*	*31*	–	–	–	–	–	–	*152*	*26*
6-9	205	31	204	25	75	33	145	33	100	28
6-9	–	–	–	–	90	41	–	–	–	–
6-16	*126*	*29*	*379*	*16*	*153*	*27*	–	–	*52*	*28*
6-23	129	25	449	13	118	21	207	31	88	26
6-30	138	29	*340*	*25*	*120*	*26*	–	–	–	–
7-7	147	33	536	21	106	24	400	30	74	27
7-14	*105*	*37*	*101*	*18*	*27*	*37*	–	–	*23*	*36*
7-21	137	32	175	17	54	30	291	29	3	18
7-28	*74*	*32*	*79*	*21*	*49*	*44*	–	–	*6*	*18*
8-4	75	39	92	21	49	42	181	24	24	29
8-4	–	–	98	20	–	–	–	–	–	–
8-25	*128*	*36*	*60*	*12*	*31*	*27*	–	–	*107*	*30*
8-25	*134*	*34*	*74*	*9*	*52*	*32*	–	–	*148*	*30*
9-22	*248*	*29*	*90*	*14*	*89*	*28*	–	–	*56*	*29*
9-22	*274*	*30*	*117*	*20*	*148*	*27*	–	–	*61*	*29*
10-20	*160*	*40*	*31*	*30*	*21*	*32*	–	–	*74*	*36*
10-20	*166*	*45*	*34*	*29*	*21*	*34*	–	–	*100*	*37*
10-20	*172*	*40*	*39*	*31*	–	–	–	–	*100*	*39*
10-20	*184*	*40*	*40*	*32*	–	–	–	–	*106*	*34*
10-20	–	–	*42*	*25*	–	–	–	–	–	–

Lake contains more sodium. They are quite different in morphometry. The shallow and unstratified Alkali Lake also lacks the marsh habitat so abundant in Falls Lake. The relatively brief freshwater history of Alkali Lake and the great fluctuations of water level may well explain the absence of the *Typha-Scirpus* marshes.

Floristically Lake Lenore and Soap Lake are quite similar, although the fresher Lake Lenore has the greater complement (Table 3). Twenty-three taxa were common to both lakes. Fourteen taxa in Lake Lenore never occurred in Soap Lake but many of these were found regularly in freshwater or semi-saline lakes in the Grand Coulee. Seven taxa in Soap Lake did not occur in Lake Lenore. Only one of these was typical of fresher water, however. The majority of the algae occurring in these saline lakes are known the world over in waters of similar salinities. A more detailed discussion of the saline flora may be found in Castenholz (1957).

TABLE 5. *Ash-free dry weight of attached materials from* saline lakes *expressed as milligrams per square meter per day and as percentage of total dry weight; two week results are in roman type, four week results are in italics; mid-dates of submergence periods are used*

Date 1955	Stations							
	L-III 0.4m top		Under-side		S-II 0.4m top		Under-side	
	mg	%	mg	%	mg	%	mg	%
3-25	24	30	–	–	–	–	–	–
4-2	*52*	*55*	–	–	*39*	*23*	–	–
4-15	*21*	*25*	–	–	*122*	*37*	–	–
4-22	–	–	–	–	245	36	–	–
4-29	*26*	*25*	*35*	*61*	–	–	–	–
5-13	*33*	*28*	*65*	*60*	–	–	–	–
5-20	63	33	71	61	–	–	–	–
6-3	24	39	34	59	219	42	–	–
6-10	*47*	*27*	*86*	*58*	–	–	–	–
6-17	82	25	42	57	74	33	–	–
6-24	*150*	*19*	*106*	*64*	*24*	*32*	*17*	*45*
7-1	35	30	81	62	49	32	–	–
7-1	–	–	–	–	74	20	–	–
7-8	*26*	*42*	–	–	–	–	–	–
7-15	53	45	24	52	42	30	–	–
7-21	–	–	–	–	*61*	*38*	*11*	*33*
7-28	49	32	–	–	86	34	–	–
7-28	62	40	–	–	–	–	–	–
8-18	*11*	*27*	*35*	*55*	*27*	*34*	–	–
8-18	*18*	*25*	*44*	*53*	*31*	*38*	–	–
9-9	226	43	101	51	96	39	35	38
9-17	*99*	*48*	*35*	*56*	*44*	*38*	*35*	*45*
9-24	171	47	21	49	101	34	51	41
10-8	246	46	–	–	533	35	26	40
10-15	*203*	*43*	*126*	*51*	*144*	*27*	*47*	*50*
10-22	650	43	84	47	490	26	74	47
11-13	–	–	–	–	*183*	*19*	*52*	*43*
11-13	–	–	–	–	–	–	*76*	*45*
12-4	–	–	–	–	221	23	–	–
12-4	–	–	–	–	282	26	–	–
12-25	*122*	*44*	–	–	*987*	*32*	–	–
12-25	–	–	–	–	*1043*	*32*	–	–

Date 1956	Stations							
	L-III 0.4m top		Under-side		S-II 0.4m top		Under-side	
	mg	%	mg	%	mg	%	mg	%
2-24	–	–	–	–	*127*	*41*	–	–
2-24	–	–	–	–	*178*	*41*	–	–
3-17	74	29	–	–	183	33	–	–
3-24	*15*	*31*	*68*	*58*	*120*	*20*	–	–
3-31	44	36	–	–	–	–	–	–
4-14	61	37	–	–	441	31	–	–
4-14	64	36	–	–	–	–	–	–
4-21	*22*	*32*	*61*	*67*	*118*	*28*	–	–
4-28	43	38	–	–	208	33	–	–
5-5	*21*	*36*	*25*	*56*	*79*	*34*	–	–
5-12	28	29	–	–	193	32	–	–
5-12	39	36	–	–	–	–	–	–
5-19	*20*	*18*	*25*	*58*	*125*	*32*	–	–
5-26	69	39	–	–	192	33	–	–
6-2	*43*	*36*	–	–	*49*	*23*	–	–
6-9	92	41	–	–	113	26	–	–
6-16	*33*	*30*	*33*	*60*	*25*	*19*	–	–
6-23	66	35	–	–	80	25	–	–
6-23	–	–	–	–	92	29	–	–
6-30	*98*	*16*	*74*	*60*	*26*	*31*	–	–
7-7	136	26	–	–	33	20	–	–
7-7	–	–	–	–	54	31	–	–
7-14	*26*	*21*	*46*	*57*	*50*	*33*	–	–
7-21	74	23	–	–	91	31	–	–
7-21	–	–	–	–	98	32	–	–
7-28	*23*	*34*	*48*	*57*	*46*	*40*	–	–
8-4	101	27	–	–	154	35	–	–
8-4	111	23	–	–	–	–	–	–
8-25	*44*	*30*	*36*	*47*	*100*	*34*	–	–
8-25	44	34	–	–	123	34	–	–
9-22	*84*	*17*	*116*	*16*	*122*	*42*	*48*	*48*
9-22	*96*	*16*	*127*	*69*	*148*	*40*	*49*	*48*
10-20	*323*	*40*	*63*	*52*	*170*	*36*	*127*	*45*
10-20	*340*	*45*	*76*	*55*	*188*	*33*	*131*	*45*
10-20	*375*	*39*	*82*	*58*	*200*	*36*	*170*	*46*
10-20	*423*	*40*	–	–	*214*	*35*	*203*	*53*
10-20	–	–	–	–	*231*	*31*	–	–

DISCUSSION OF THE GLASS PLATE TECHNIQUE

Submergence time

Results obtained from 2- and 4-week plates were usually comparable during summer periods of low production in both classes of lakes (Tables 4 and 5). During greater spring production in freshwater lakes somewhat higher rates were generally obtained with 4-week plates (Table 4). However, during high production in saline lakes 2-week plates definitely showed higher production (Table 5).

In general a 2-week submergence period is empirically more satisfactory since a shorter period records more fluctuations of production rate and more accurately pinpoints the time. A period of less than 2 weeks would be perhaps even more desirable. However, if the period were shortened to only a few days it is probable that the number of algal cells settling on the plates would exaggerate the production rate or growth increment values.

Patrick and co-workers (Patrick *et al.* 1954) found that the number of diatom species occurring on 1-week slides was similar to that on 2-week slides. A significantly smaller number occurred on 4-week slides. The greater accumulation of debris and other organisms and the crowding out of some forms by fast growing diatom species were given as possible explanations for the 4-week results. Patrick concluded that two weeks seemed to be the optimum period of submergence in the rivers studied to date. It has been pointed out, however, that submergence time should probably vary somewhat according to the type of lake or river, water temperature, season, and purpose of the experiment (Patrick *et al.* 1954, and Newcombe 1949, 1950). Patrick's group was not studying production but floras indicative of river conditions. Newcombe, studying production, suggested that during periods of low production either larger slides or longer periods of submergence be used in order to obtain at least 3–5 mg of ash-free dry weight per slide. The glass plates used in the present study obtained weights well in excess of this after two weeks of submergence even during lowest production.

One would expect production rate results to decrease with loss from mineralization, with peeling and rising because of trapped gases, with sloughing off of dead and loose cells by wave movements, and with grazing by animals. These factors would distort production rate values more with longer submergence periods. Peeling was observed only on plates that had been submerged longer than four weeks in freshwater. Gastropods were present in the freshwater lakes only but were not common, at least in the upper 2 m. Grazing of attachment materials on plates by gastropods was rarely observed. Since higher production rate values in freshwater lakes were obtained from 4-week plates than from 2-week plates during periods of high production, it might be assumed that real production rates were even higher and that the reduction factors were probably very slight. Therefore, four weeks is probably not too long a period of submergence but it is certainly less sensitive than a 2-week period. In saline lakes, however, the low values of 4-week plates indicate a large amount of reduction. Here it appeared that loss by wave action was the main factor after the thickness of attachment materials had increased beyond a period of 1.5 to 3 weeks. Many of the algae, particularly the blue-green, in the saline lakes were loosely attached to the substrate.

The scraping of glass plates

As mentioned earlier (see Materials and Methods) it was the usual practice to return scraped plates to the water. Sometimes unused plates were used as replicates. In such cases no significant differences in results were found. It might be supposed that greater quantities of attachment materials should be obtained from used plates than from unused ones after a 2- or 4-week submergence period. The washed plates seldom dried completely before resubmergence. It is also questionable whether a short period of desiccation would affect the viability of most diatoms (Evans 1958). Scraping cannot be 100% efficient, and the diatoms remaining on used plates would have some start. Since results indicate

otherwise, it would seem that the "seeding-on" of diatom cells must be rapid enough to colonize the plate surface uniformly in a short time. Perhaps, if both types of plates had been examined after only a few days a significant difference would have been found.

Glass selectivity

Most of the epilithic algae became attached to glass as well as to rocks. The rapidly growing green alga *Ulothrix aequalis* in Falls Lake did not attach to glass except when the plates were located at the water-air interface. This, however, was the only region of attachment on rocks as well. The positive phototaxis of zoospores was the probable factor involved. *Cladophora fracta* in freshwater lakes did not attach to glass. This was probably due to the perennial nature of *Cladophora* filaments and the probably infrequent production of swarmers (Castenholz 1957). Many of the slowly growing, rock encrusting blue-green algae (*e.g., Amphithrix, Calothrix, Entophysalis*) did not occur commonly on 2- or 4-week plates. This was apparently due to the time factor, since plates exposed for much longer periods showed a development of these genera. The rock encrusting green alga *Gongrosira* also falls into this category.

The results of Patrick *et al.* (1954) also show that glass is not selective as far as diatoms are concerned. The species collected by their apparatus . . . . "are from 75 to 85% the same as those taken by thorough collecting of the region by a diatomist at the time the slide is removed from the apparatus. Those diatoms not common to the slide and to the collections made by the diatomist were mostly represented by less than four specimens; 95% of those represented by 8 or more specimens were common to both." In all the lakes of the Lower Grand Coulee no epilithic or epiphytic diatom species were excluded from glass plates. It was also apparent that the relative abundance of the various species on the glass plates was similar to that on the rock substrate in the immediate vicinity.

Although the ordinary window glass used in this investigation appeared non-selective, it is possible that a rougher surface would be required for permanent settling and firm attachment of some species of algae. In rather crude preliminary experiments sand-blasted (frosted) and normal glass microscope slides were submerged horizontally in metal staining racks. After both two and four weeks of submergence no difference in quantity and composition of attached algae was apparent. If a bacterial film is formed very quickly on a glass surface, attachment of small forms, such as diatoms, may not be much affected by the nature of the glass surface itself.

It is recommended that in future studies of this sort a direct comparison be made between production rate on glass plates and on submerged sterile rocks of the type found in the lake studied. Finding rocks of sufficient size to present a flattened side large enough in area to be usable is apt to be difficult. A further difficulty is removing the attachment material from an irregular and pitted rock surface in a quantitative manner.

Comparison of horizontal and vertical surfaces

In the present study it was found that the weight of material from vertically and horizontally placed plates in Falls Lake was in a ratio of 1:12.4 during the spring and 1:6.2 in the summer. The results of Newcombe (1950) were somewhat similar, 1:6.6 in late summer and early fall and 1:3 in late fall. Newcombe also noted that the loss during removal of vertical slides from the water may exceed the amount that remained. Horizontal slides could be removed with a minimum of surface disturbance. It is obvious, however, that horizontal surfaces will collect more of the organic detritus that settles out from suspension. This seemed a negligible factor in the fresh-water lakes of the Grand Coulee. Undisturbed living material was examined periodically under the microscope. During high production in the spring nearly all of the material was composed of attached diatoms. In the saline lakes, however, a considerable amount of organic detritus was collected by the horizontally placed plates.

The attachment material produced on the underside of glass plates was also collected regularly from plates mounted on tripods. The ash-free dry weight of underside material sometimes equaled or even exceeded the weight of upperside material during low production periods in both the freshwater and saline lakes (Table 5). During high production, however, upperside production predominated, as would be expected because of greater light absorption. In most cases the species composition was similar on both surfaces. Newcombe (1950) found that the amount of attachment material on the underside of slides was generally small.

Sedimentation of inorganic particulate matter on horizontal glass plates was of some importance in all the lakes, but was considered of major importance only during the turbid period in Alkali Lake in spring 1955, and occasionally in the saline lakes. Of the materials collected from the upperside of glass plates, the ash varied usually from 50% to about 85% of the dry weight (Tables 4 and 5). These figures were compared with the percentages of ash on the undersides where inorganic sediment would be nearly absent. The underside ash percentages of nearly pure diatom material were fairly constant for each lake throughout the year and were thus considered the "ideal" ash percentages. They amounted to about 47% in Falls Lake, 48% in Alkali Lake, 42% in Lake Lenore, and 55% in Soap Lake. This compares fairly well with percentages of ash from pure diatom material: *Amphipleura rutilans*—46%, *Navicula torquatum*—35% (Burlew 1953). By subtracting the "ideal" ash percentages from those obtained from the uppersides, estimates of the inorganic sediment deposited on top were made. The sediment thus varied from practically 0% to 40% of the dry weight of the material. The percentage ash from the upperside was never less than that obtained from the underside of the same plate. It was often found that greater sedimentation occurred on shallower plates than on deeper ones (Table 4). Greater sedimentation occurred in freshwater lakes during high water periods of spring than during low water periods of summer and early fall (Table 4).

TABLE 6. *Ash-free dry weights as milligrams per square meter per day from replicate glass plates*

Station	No. of plates	$\bar{X}$	s	C as %
Falls-V (surface)	5	37.2	± 9.4	25.3
Falls-I (0.4 m)	4	170.5	±17.3	10.1
Alkali-I (0.4 m)	4	95.0	±24.2	25.5
Lenore-III (0.4 m)	4	365.3	±77.9	21.3
Soap-II (0.4 m)	5	200.6	±43.8	21.8

Replicate plates

At most stations, at least three plates were used at each depth in order to collect 2- and 4-week plate material at bi-weekly intervals. At some stations extra plates were used periodically as replicates (Table 4 and 5 and Figs. 2–10). Fewer than four replicates were used at most times, but four or five replicates of 4-week plates were used at the main stations in all lakes for the collection on November 3, 1956. The mean ash-free dry weights expressed in mg/m²/day, the standard deviations (s), and coefficients of variation (C) are given in Table 6. As expected, variations are numerically greater with higher weights, but percentage variations are rather similar. Although 25% in itself represents a rather large degree of variation, it may be seen that it would not distract much from the major trends shown by the curves (Figs. 2–10). Whenever duplicate or replicate plates were used at other dates the results are usually well grouped. It is the author's opinion that single plate results may be considered reliable within ±25% of the value obtained, particularly if no disturbances are noted on the plates in the field.

A more widespread use of many plates at a single station was prevented by insufficient space on the rock ledges and also by barely adequate time to sample all stations in the four lakes. Some attempts at setting up many replicates were spoiled by vandals who destroyed entire sets.

Suitability of the method in the saline lakes

The glass plate method was not so well adapted to use in the saline lakes. In the freshwater lakes the epilithic vegetation was dominated by diatoms which readily attached to glass. Diatoms were important

plate organisms in the saline lakes as well, but there were also very important epilithic species of blue-green algae that commonly attached to glass in the 2- or 4-weeks. Some blue-green algal species were only slightly adhesive to plates and rocks. Generally these were species more characteristic of the benthoplankton, such as *Anacystis marina* and *Plectonema nostocorum*. It was difficult to remove plates from the water without losing some of this material. Chironomid larvae were frequently found encased on the surface of plates. In Lake Lenore these organisms never amounted to more than 5% of the ash-free dry weight. However, in Soap Lake, chironomids sometimes accounted for as much as 30%, particularly in the spring.

Another complication encountered in the saline lakes was the weakly silicified nature of the diatom frustules. The walls of most species were completely deformed during ashing. Consequently the counting method could not be used. This difficulty was compensated for by the fact that only a few species of diatoms occurred commonly, and these were of approximately the same cell size. Thus, rough estimates of dominance were made before ashing.

The two saline lakes had a larger surface area than the two freshwater lakes. The significantly greater wave action in larger lakes probably has a greater reducing effect on attachment materials on glass plates. It was also noted in the larger freshwater lakes, such as Blue Lake and Park Lake, that the spring diatom carpet was not so heavy as in Falls Lake and that epilithic *Cladophora* was not so luxuriant in the summer. It may be surmised that the greater wave action in the larger lakes has a modifying influence on such features. Jorgensen (1948) found similar differences between large and small lakes in Denmark.

General application

Although there are several limitations to the glass plate production technique, the author believes that it may be applied successfully to a large number of lake and stream types, as well as to marine situations. However, the present type of quantitative procedure in analyzing species composition is practical only where diatoms predominate, since it is very difficult to mix thoroughly the mass of attachment materials before ashing at a high temperature.

It is possible that glass production results may be of some value in characterizing the whole primary production of a lake, although many members of the phytoplankton do not attach readily to a firm substrate. Simultaneous studies of planktonic and attached algal production would be of interest. Certainly the attached algae should not be ignored in studies of primary production, particularly in smaller bodies of water where their contribution may be great.

DISCUSSION OF SEASONAL CHANGES

A comparison of diatom production in Falls Lake and Alkali Lake brings out several quantitative and qualitative differences. From the results of the one station in Alkali Lake it would appear, however, that total annual production of organic matter per unit area in the upper meter was similar to that of Falls Lake. The seasonal similarities were such that a bimodal production curve with a higher maximum in spring was evident in both lakes (Figs. 2–6 and 8). It may be seen that the spring diatom outburst was usually initiated at a lower temperature (5°–12°C) than the fall outburst (15°–17°C). It is also true that light intensity and length of day are greater in April and May than in October or November. There exist, then, widely different temperature-light values at the initiation time of the two main diatom pulses although some of the same species are involved. A similar situation appears to be common in lakes throughout the temperate world (Patrick 1948). This pattern is by no means a consistent feature of all types of lakes, however. Pennak (1946, 1949) pointed out that bimodal planktonic diatom curves are most characteristic of medium to large deep lakes. In several studies of small to medium size lakes in Colorado he noted no characteristic spring or fall pulse. Instead, one, two, or three pulses occurred at various times of year.

It may be seen that the seasonal fluctua-

tion of overall diatom production curves is generally a function of the combined independent variations of several species. The seasonal periodicities of only a few of the diatom taxa occurring in the Lower Grand Coulee have been noted in other temperate waters. In making comparisons one must bear in mind that there is always a possibility or probability that two or more ecotypes or genetic types are involved.

The role of certain species during high production periods differed somewhat in Falls Lake and Alkali Lake. *Cymbella affinis, C. cistula,* and *C. mexicana* were abundant species of fall, winter, and spring on shallow rocks in Falls Lake. All were present in Alkali Lake but never in any great abundance. Blum (1957), on the other hand, noted that *C. affinis* was predominantly a "summer" form in a Michigan stream. *C. cistula* is widespread throughout the world, but little has been said about its seasonal periodicity. *C. mexicana,* however, is apparently restricted to western North America, and no other seasonal information is available. *C. mexicana* was the most conspicuous "spring" diatom of Falls Lake, but it also occurred in some abundance during the summer in deeper habitats. A similar distribution of certain diatoms was noted by Godward (1937) and Rohde (1948).

Cymbella turgida and *C. ventricosa* were common during the spring pulse in Falls Lake but occurred abundantly in the summer only in Alkali Lake. Similarly, Godward (1937) and Butcher (1932a) found *C. ventricosa* as a spring form in English lakes and streams, while in a Michigan stream it was most abundant in summer (Blum 1957).

Synedra acus and *S. ulna* were characteristic "spring" forms of both freshwater lakes. Reports of Butcher (1932a) and others confirm this pattern. Blum (1957), however, found both species most abundant in summer.

Diatoma elongatum, D. vulgare, and *Gomphonema olivaceum* were "spring" species abundant in Alkali Lake only. The reports of several workers confirm that these species are restricted to cold water periods (*e.g.,* Blum 1957, Butcher 1932a, Godward 1937).

The rather dramatic replacement of "spring" diatom species on shallow rocks by *Epithemia turgida* and *E. sorex* in summer has (to this author's knowledge) not been discussed elsewhere. There is little information on the seasonal cycles of other species of diatoms common in the Grand Coulee. Bock (1953), Budde (1928), Butcher (1946), Jürgensen (1935), and Niessen (1956) present some additional information from studies in Europe.

Since only a small portion of the environmental complex has been studied it is impossible to offer a positive statement regarding the factors causing the initiation, maintenance, and depletion of algal pulses in these lakes. It would seldom be possible to designate a single factor as the sole agent involved, and it is probable that an interplay of many factors is involved. Probably different combinations of chemico-physical factors are effective from one type of water to another, from one season to the next, and from one species or ecotype to another.

The seasonal cycles of production in the saline lakes were conspicuous for the large fall pulse which was initiated at rather high temperatures (15°–20°C) in both lakes. A large winter pulse followed by a spring pulse was characteristic of Soap Lake only. Yet, the pulses of all three seasons in Soap Lake were dominated by the same species and varieties of *Nitzschia* and *Amphora.* The same taxa (plus *Amphora coffeaeformis*) were involved in the fall pulse in Lake Lenore. The absence of a winter peak in Lake Lenore can probably be ascribed to the presence of an ice and snow cover. The absence of a spring peak in Lake Lenore is unusual, particularly since Anderson (1958) noted a spring phytoplankton pulse.

An extensive literature on the salinity and pH tolerances of diatom species exists. Rather strict halobien and pH spectra have been established (Patrick 1948). The floristic composition of Lake Lenore and Soap Lake agree well with the established order. However, there is practically no information available on the seasonal periodicity of the saline diatoms in other regions.

REFERENCES

ABDIN, G. 1949. Benthic algal flora of Aswan Reservoir (Egypt). Hydrobiol., **2**: 118–133.

ANDERSON, G. C. 1958. Seasonal characteristics of two saline lakes in Washington. Limnol. Oceanogr., **3**: 51–68.

ANDERSON, G. C., G. W. COMITA, AND VERNA ENGSTROM—HEG. 1955. A note on the phytoplankton–zooplankton relationships in two lakes in Washington. Ecol., **36**: 757–759.

BISSONNETTE, T. H. 1930. A method of securing marine invertebrates. Science, **71**: 464–465.

BLUM, J. L. 1957. An ecological study of the algae of the Saline River, Michigan. Hydrobiol., **9**: 361–408.

BOCK, W. 1953. Floristisch-ökologische Untersuchung der Algenvegetation periodischer Gewässer im südlichen Teil des Maindreieckes. Arch. Hydrobiol., **47**: 9–74.

BRETZ, J. H. 1932. The Grand Coulee. Am. Geogr. Soc., Spec. Publ. No. **15**. 89 pages.

BUDDE, H. 1928. Die Algenflora des Sauerländischen Gebirgsbaches. Arch. Hydrobiol., **19**: 433–520.

BURLEW, J. S. (ed.) 1953. Algal culture: from laboratory to pilot plant. Carnegie Inst. of Wash. Publ. **600**, p. 286.

BUTCHER, R. W. 1932a. Studies on the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river bed. Ann. Bot., **46**: 813–861.

———. 1932b. An apparatus for studying the growth of epiphytic algae with special reference to the River Tees. Trans. North. Naturalist's Union, **1**: 1–15.

———. 1946. Studies in the ecology of rivers. VI. Algal growth in certain highly calcareous streams. J. Ecol., **33**: 268–283.

CASTENHOLZ, R. W. 1957. Seasonal changes in the algae of freshwater and saline lakes in the Lower Grand Coulee, Washington. Ph.D. Thesis, State College of Washington.

CHOLODNY, N. 1930. Über eine neue Methode zur Untersuchung der Bodenmikroflora. Arch. f. Mikrobiol., **1**: 620–652.

COE, W. R., AND W. E. ALLEN. 1937. Growth of sedentary marine organisms on experimental blocks and plates for nine successive years at the pier of the Scripps Institution of Oceanography. Bull. Scripps Inst. Oceanogr. Tech. Ser., **4**: 101–136.

COOKE, W. B. 1956. Colonization of artificial bare areas by microorganisms. Bot. Rev., **22**: 613–638.

DAUBENMIRE, R. F. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecol. Monogr., **12**: 53–79.

EVANS, J. H. 1958. The survival of freshwater algae during dry periods. Part I. An investigation of the algae of five small ponds. J. Ecol., **46**: 149–167.

GODWARD, M. 1937. An ecological and taxonomic investigation of the littoral algal flora of Lake Windermere. J. Ecol., **25**: 496–568.

HENTSCHEL, E. 1916. Biologische Untersuchungen über den tierischen und pflanzlichen Bewuchs im Hamburger Hafen. Mitt. Zool. Mus. Hamburg, **33**: 1–172.

———. 1925. Abwasserbiologie. Abderhalden's Handb. Biol. Arbeitsmethod., **9**(2): 233–280.

IVLEV, V. S. 1933. Ein Versuch zur experimentellen Erforschung der Ökologie der Wasserbiocönosen. Arch. Hydrobiol., **25**: 177–191.

JORGENSEN, E. G. 1948. Diatom communities in some Danish lakes and ponds. K. Danske Vidensk. Selsk. Biol. Skr., **5**(2): 1–140.

JÜRGENSEN, CHARLOTTE. 1935. Die Mainalgen bei Würzburg. Arch. Hydrobiol., **28**: 361–414.

NEWCOMBE, C. L. 1949. Attachment materials in relation to water productivity. Trans. Am. Micros. Soc., **68**: 355–361.

———. 1950. A quantitative study of attachment materials in Sodon Lake, Michigan. Ecology, **31**: 204–215.

NIESSEN, HERTA. 1956. Ökologische Untersuchungen über die Diatomeen und Desmidiaceen des Murnauer Moores. Arch. Hydrobiol., **51**: 281–375.

PATRICK, RUTH. 1948. Factors effecting the distribution of diatoms. Bot. Rev., **14**: 473–524.

———, M. H. HOHN, AND J. H. WALLACE. 1954. A new method for determining the pattern of the diatom flora. Notulae Naturae, No. **259**, 12 pp.

PENNAK, R. W. 1946. The dynamics of freshwater plankton populations. Ecol. Monogr., **16**: 339–391.

———. 1949. Annual limnological cycles in some Colorado reservoir lakes. Ecol. Monogr., **19**: 233–267.

RAWSON, D. S., AND J. E. MOORE. 1944. The saline lakes of Saskatchewan. Can. J. Res., Sec. D, **22**: 141–201.

ROHDE, W. 1948. Environmental requirements of fresh-water plankton algae. Experimental studies in the ecology of phytoplankton. Symbolae Bot. Upsalienses, **10**(1): 1–149.

SCHEER, B. T. 1945. The development of marine fouling communities. Biol. Bull., **89**: 103–121.

THOMASSON, H. 1925. Methoden zur Untersuchung der Mikrophyten der limnischen Litoral- und Profundalzone. Abderhalden's Handb. Biol. Arbeitsmethod., **9**(2): 681–712.

WHITTAKER, R. H., AND C. W. FAIRBANKS. 1958. A study of plankton copepod communities in the Columbia Basin, Southeastern Washington. Ecol., **39**: 46–65.

WITHROW, R. B., AND ALICE P. WITHROW. 1953. A linear recording AC conductance bridge for measuring salt exchange in plants. Physiol. Plantarum, **6**: 444–450.

YOUNT, J. L. 1956. Factors that control species numbers in Silver Springs, Florida. Limnol. Oceanogr., **1**: 286–295.

CHLOROPHYLL DERIVATIVES IN SURFACE MUDS FROM THE ENGLISH LAKES[1]

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ABSTRACT

Chlorophyll derivatives, total carbon, and total sulfur have been estimated in surface muds from the depths of five widely differing bodies of water. All three components increase in passing from muds of large infertile lakes, with waters low in phytoplankton and poor in lime and potash, to muds of smaller and more fertile lakes, with big phytoplankton crops and more plentiful supplies of lime and potash in their waters. Certain differences in the absorption spectra of acetone extracts may be related to the balance between organic materials originating inside and outside the lakes, and to the length of time they spend in an oxidizing environment.

INTRODUCTION

The presence of chlorophyll degradation products in lake muds has been recognized for many years (Vallentyne 1957 gives many references), but little is known of their abundance in muds from lakes of different kinds. Therefore it was thought worthwhile to investigate this matter in the English Lake District, where a wide variety of lakes and tarns has been examined from many different points of view.

For the present purpose five lakes of widely differing fertility were studied:

Wastwater and Ennerdale Water. Both are rather deep lakes, in which the hypolimnion contains oxygen throughout the period of stratification. The waters are low in lime and potash, and phytoplankton is sparse.

Windermere, North Basin. A large deep lake, the hypolimnion of which remains oxygenated throughout its existence. The water contains moderate amounts of lime and also of phytoplankton.

Esthwaite Water. A smaller shallow lake, in which the hypolimnion becomes completely de-oxygenated near the mud surface. The water is richer in lime and potash than those above, and the phytoplankton crops are also relatively large.

Priest Pot. A small and very shallow pond at the north end of Esthwaite Water, in which oxygen disappears from the water above the mud in summer. The water of this pond is richest of all in lime and potash, and the phytoplankton is also extremely dense. Although no quantitative estimates are available, all through the summer it was necessary to use a Buchner filter to clear the waters for chemical analysis, and even then the rate of filtration was slow.

METHODS

From the deepest parts of these lakes the surface 5 cm of mud were collected with a Jenkin surface sampler (Mortimer 1942, Fig. 22), and analyzed for chlorophyll derivatives within 24 hours. Plankton and sedimentary debris from Esthwaite Water were also analyzed. The samples were then dried at 100–110°C, and later total carbon and total sulfur were estimated, since the contents of these elements might also be expected to vary in relation to lake fertility.

One to two grams of fresh mud were shaken mechanically for three periods of 5–10 min. with successive 20–30 ml portions of 90% acetone, the extracts being filtered and the residues leached with 90% acetone to give a final filtrate of 100 ml. The plankton samples had to be more highly diluted. Absorption spectra were then measured (at 10-mμ intervals or less) within a few hours

[1] This work was done while the writer was on the staff of the Freshwater Biological Association, Ambleside, England, and he is indebted to Mr. David Driver for help with the analyses, to Mr. G. J. Thompson and the laboratory staff for collecting the samples, and to Mr. F. J. H. Mackereth for advice on techniques. The statements on phytoplankton abundance are based on discussions with Dr. J. W. G. Lund. The chemical analyses of lake waters given in Table 1 were provided through the courtesy of Mr. Mackereth and Mr. J. Heron.

TABLE 1. *Physical and chemical properties of the lakes and their waters*

	Area	Max. depth	Total salts	Na	K	Ca	Mg	HCO_3	Cl	SO_4	NO_3
	km^2	m	in milli-equivalents per liter								
Wastwater	2.9	79	0.31	0.15	0.01	0.09	0.07	0.05	0.16	0.10	0.006
Ennerdale Water	2.9	45	0.33	0.17	0.01	0.09	0.07	0.05	0.18	0.10	0.005
Windermere North Basin	8.2	67	0.51	0.16	0.01	0.27	0.07	0.17	0.17	0.14	0.018
Esthwaite Water	1.0	16	0.75	0.20	0.02	0.41	0.12	0.31	0.20	0.20	0.013
Priest Pot approx.	0.01	4.5	1.09	0.25	0.08	0.62	0.15	0.66	0.23	0.19	0.002

in a Unicam SP 500 spectrophotometer, with glass cells and using the solvent as blank. No basic substance was added to the sample to preserve chlorophyll from conversion to pheophytin, as the absorption spectrum of the extract of living planktonic algae showed little evidence of such a conversion in the short time between extraction and spectrophotometry of the sample. Chlorophyll and its derivatives were estimated from the absorption peak at about 667 mμ, in arbitrary units, one unit being taken as equivalent to an optical density of 0.1 in a 1-cm cell when dissolved in 100 ml of solvent (*cf.* Vallentyne 1955), after subtracting an approximate correction factor obtained by drawing a freehand base-line to the absorption curve between 550 and 750 mμ (*cf.* Orr and Grady 1957). Aliquots of the muds were then dried at 100–110°C to allow expression of results on the dry weight basis, and these were used for the estimation of total carbon and total sulfur. Carbon was analyzed gravimetrically by dry combustion (free carbonate being absent), and sulfur as sulfate, using a new technique devised by F. J. H. Mackereth (in preparation).

RESULTS

As previously indicated, the five lakes differ considerably, and Table 1 shows the range of variation in some of their physical and chemical properties. The contents of total carbon, total sulfur, and chlorophyll derivatives in surface muds from the deepest parts of these lakes are shown in Table 2, from which it appears that all three variables follow similar trends; high values characterize the more fertile lakes with abundant phytoplankton and waters rich in lime and potash. However, on the dry weight basis

TABLE 2. *Chlorophyll derivatives, total carbon and total sulfur in the lake muds*

	Carbon % dry weight	Sulfur % dry weight	Chlorophyll derivatives units per g dry weight	Ratio of optical densities 410/350 mμ
Wastwater	7.2	0.18	0.21	0.7
Ennerdale Water	6.6	0.19	0.24	0.9
Windermere, North Basin	8.7	0.37	0.83	1.0
Esthwaite Water	11.6	0.61	1.37	1.4
Priest Pot	18.9	1.22	6.88	1.8

total carbon increases only about three-fold in passing from the lake mud with the lowest content to that with the highest, while total sulfur increases nearly seven-fold, and chlorophyll derivatives over thirty-fold. Expressed in terms of organic content, sulfur increases from less than 3% of carbon in muds from Wastwater and Ennerdale Water to more than 6% in the mud of Priest Pot. Similarly, in muds from the former lakes there are only about 3 units of chlorophyll derivatives per gram of carbon, while in Priest Pot there are 36 units. These data suggest that the concentration of chlorophyll derivatives in the mud may be a more sensitive index of lake fertility than the concentration of either carbon or sulfur. They do of course refer only to single samples, but others collected later in a slightly different way confirmed the general trend observed in this sequence of strikingly different lakes.

The above levels of chlorophyll derivatives, expressed as units per gram of carbon, may be roughly compared with that of about 250 units of chlorophyll per gram of carbon in the living phytoplankton diatom *Melosira italica subarctica*. After centrifuging and standing for 3–4 days at laboratory temperature, the concentration of chlorophyll de-

rivatives in the dead alga (as measured by the present technique) was only about half the above value. Leaves from three living land plants yielded from 19 to 55 units of chlorophyll per gram of carbon, with the latter figure declining to 21 units of chlorophyll derivatives after the leaves were ground up and stored moist for eight days in an open dish (Gorham 1959). It should be pointed out here that chlorophyll and pheophytin cannot be compared strictly on this basis, since the mere conversion of chlorophyll to pheophytin lessens light absorption of acetone extracts by about 30% (Katz and Shore 1955). The fact that the absorbancy values declined by about 50% in the case of *Melosira* and over 60% in the case of the oak leaves does however suggest some further degradation in addition to the conversion to pheophytin.

In yet another rather crude comparison debris caught over a ten-day period in March, in sediment traps (Tutin 1955) set out at depths of 1 and 11 m in Esthwaite Water, yielded concentrations of chlorophyll and its derivatives amounting to 80 and 75 units per gram of carbon, respectively, compared with the 12 units in surface mud. It should be pointed out however that in autumn the debris sedimenting in Esthwaite Water might well include a much greater proportion of terrestrial plant material of lower chlorophyll content.

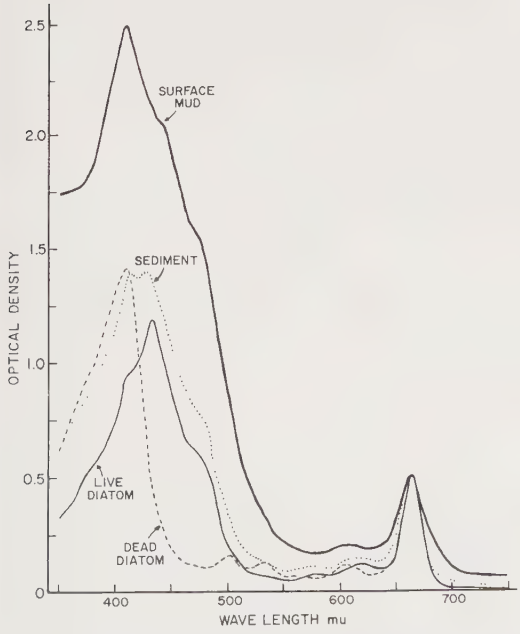

FIG. 1. Absorption spectra of acetone extracts from (a) living and (b) dead diatoms, and from (c) sedimenting debris and (d) surface mud, all collected in Esthwaite Water.

While the concentrations of chlorophyll derivatives in the various lake muds are of paramount interest, some consideration of the whole absorption spectra of the acetone extracts is not without value. Figure 1 compares spectra from living *Melosira*, dead *Melosira*, debris caught in the Esthwaite sediment trap at 11 m depth, and the top 5 cm of Esthwaite mud, all of these being adjusted to give the same absorption for the red peak between 665 and 670 mμ, from which the concentrations of chlorophyll derivatives were estimated.

In comparing living with dead *Melosira*, the major change observed is a shift of the maximum absorption peak from about 435 mμ back to about 410 mμ, together with a relative increase in the absorption recorded for this major peak. In addition the minor hump at about 620 mμ shifts back to 605 mμ, and two new minor humps appear at about 530 mμ and 505 mμ. There is also a marked decrease in absorption between about 530 and 490 mμ. The net result of all these changes is that the spectrum comes to resemble closely that for pheophytin *a*, which Orr and Grady (1957) suggest as the main chlorophyll derivative in marine sediments. In this connection it may also be noted that the plankton spectrum illustrated by Vallentyne (1955) bears a distinct resemblance to those of dead *Melosira* and pheophytin *a*.

The material caught in the sediment traps, which were set out before stratification, clearly includes both chlorophyll and its derivatives, as evidenced by the dual nature of the absorption maximum toward the violet end of the spectrum. This suggests that a good deal of chlorophyll decomposition takes place before the dead plant material is deposited on the mud surface, and J. F. Talling (private communication) has added weight to this conclusion by his observation that after stratification dying

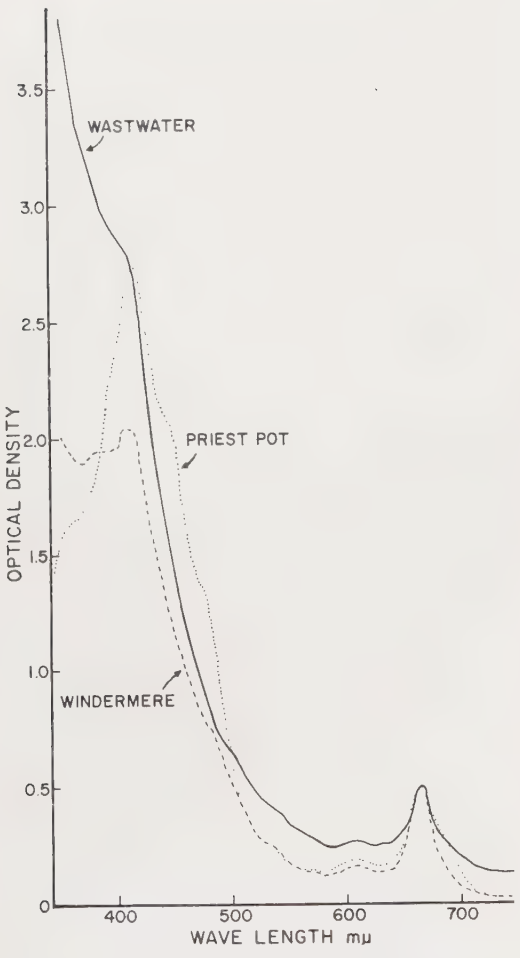

FIG. 2. Absorption spectra of acetone extracts from the surface muds of Wastwater, Windermere North Basin, and Priest Pot.

Asterionella populations collected below the thermocline exhibit a shift of the major absorption peak at about 435 mμ to distinctly lower wave lengths.

If the absorption spectrum of Esthwaite mud is now examined in relation to the others illustrated in Figure 1, it will be seen to resemble that of dead *Melosira,* although it shows a greater absorption at all wave lengths other than the red peak made arbitrarily equal. This greater absorption is especially marked between about 450 and 490 mμ, where the extract of the living alga absorbs considerable light, but those of the dead alga and of pheophytin *a* do not. The reasons for these discrepancies are not apparent, but substances other than chlorophyll and its derivatives are certainly present in the acetone extracts and must affect the absorption spectra.

Figure 2 compares spectra of muds from three of the five lakes. Considerable differences are evident, particularly toward the violet end of the spectrum where the less fertile lakes exhibit distinctly greater light absorption. This difference is best illustrated by calculating the ratios of optical densities at 410 to those at 350 mμ (Table 2). These show a steady rise in passing from the infertile lake Wastwater (ratio 0.7) to the very fertile pond Priest Pot (ratio 1.8). The ratio is even higher in both living and dead *Melosira* (ratios 2.9 and 2.3 respectively), while the sediment traps (ratios 2.0 and 2.1) yield values intermediate between those of the algal materials and the muds.

Strong light absorption at 350 mμ is also noticeable in acetone extracts of terrestrial plants and of woodland soils; and the absorption spectrum of the Wastwater mud extract closely resembles those of aerobic woodland *mull* and *mor* humus layers (*cf.* Gorham 1959). This fact might be taken to suggest that a good deal of the organic matter in Wastwater sediments enters the lake from its drainage basin, in contrast to either Esthwaite Water or Priest Pot, where the large phytoplankton crops provide a relatively more abundant supply within the lake basins themselves. It is also likely that any plankton sedimenting in the less fertile lakes will be exposed to oxidation for a longer period than in the more fertile waters, which appear to have thinner oxidized microzones at their mud surfaces (*cf.* Mortimer 1942).

DISCUSSION

While these lakes exhibit definite relationships between the amounts of chlorophyll derivatives, total carbon, and total sulfur in their muds, the richness of their waters in nutrients such as lime and potash, and the abundance of their phytoplankton, the exact reasons for these correlations remain obscure. Many factors undoubtedly interact to determine the concentrations of

these mud constituents, among which the following may prove to be of chief importance, and to deserve detailed investigation: (1) the initial contents in the organisms contributing to the lake sediments, (2) the rapidity with which the dead organisms become sedimented and then buried in the mud, (3) the amounts and nature of the mineral materials sedimenting in the lakes at the same time, and (4) the degree of bacterial activity in the lakes and their muds, and hence the concentrations of oxygen there. The present study merely indicates that certain relationships do exist, and it is hoped that they may be of use in interpreting problems of lake development.

REFERENCES

GORHAM, E. 1959. Chlorophyll derivatives in woodland soils. Soil Sci., **87**: 258–261.

KATZ, M., AND V. C. SHORE. 1955. Chlorophyll and pheophytin in conifer leaves in relation to the diagnosis of gas damage and needle blight disease in the Sudbury District. Report to Special Sulphur Dioxide Investigating Committee. Ottawa, 1955.

MORTIMER, C. H. 1942. The exchange of dissolved substances between mud and water in lakes. J. Ecol., **30**: 147–201.

ORR, W. L., AND J. R. GRADY. 1957. Determination of chlorophyll derivatives in marine sediments. Deep-Sea Res., **4**: 263–271.

TUTIN, W. 1955. Preliminary observations on a year's cycle of sedimentation in Windermere, England. Mem. Ist. Ital. Idrobiol., suppl., **8**: 467–484.

VALLENTYNE, J. R. 1955. Sedimentary chlorophyll determination as a paleobotanical method. Can. J. Bot., **33**: 304–313.

———. 1957. The molecular nature of organic matter in lakes and oceans, with lesser reference to sewage and terrestrial soils. J. Fish. Res. Bd. Canada, **14**: 33–82.

DISSOLVED OXYGEN IN SWEETWATER LAKE

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ABSTRACT

In Sweetwater Lake, near San Diego, California, vertical distribution of dissolved oxygen was observed to be highly stratified during the early summer months. With the lake at a maximum depth of about 32 ft, the lower 5 to 10 ft were devoid of oxygen by early July but mid-depths and upper levels remained well-oxygenated throughout the period of observation. The pattern of oxygen distribution in the lake appeared to reflect the prevailing summer circulation which consisted of rapid down-wind movement at the surface with counter-currents at mid-depths and smaller circulation cells at lower depths. Rising summer temperatures caused an increase in the depth of the upper layer of water saturated or supersaturated with oxygen. The drop in solubility of oxygen due to heating of the surface layers of water was proportionally greater than the decrease in oxygen content, producing an increase in saturation values. Thermal stratification seemed to be sufficient, by reduced vertical mixing, to maintain the lake in a condition of oxygen-rich epilimnion and oxygen-depleted hypolimnion.

Serial observations showed a diurnal cycle of rising oxygen content in the surface layers in late afternoon and evening, probably the results of the photosynthetic activity of the phytoplankton and the circulation of high oxygen water from the shallow end of the lake.

Simultaneous sampling of the water at various depths for oxygen analysis and measurement of light transmission with a hydrophotometer produced no correlation between oxygen content and turbidity. Simultaneous measurement of sound velocity, attenuation and oxygen content also produced no conclusive results.

INTRODUCTION

Of all the chemical conditions in lakes and oceans, oxygen content has probably received the most attention. However, comparatively little has been done by way of intensive, repeated investigation of the oxgen in a single location such as that undertaken in this study. Johnson (1949) has reported on a study of the plankton of Sweetwater Lake, and McEwen (1941) has worked on the hydrographic conditions of the lakes of the region, but apparently there has been no previous investigation of specific chemical conditions.

In the study of which this report is a part, the temperature, turbidity, sound velocity, circulation, and daily changes were studied at Sweetwater Lake for several months from April to August, 1957, with the general objective of discovering relationships between these conditions and acoustical properties of the water. The lake is located near San Diego and is a mile and three-quarters in length situated in an east-west direction (Fig. 1). It has a gently sloping basin with a maximum depth at the time of the study of about 32 ft at the west end near the dam. Its proximity to the sea, which is only 10 miles away, makes the daily sea breezes one of the more important influences on its pattern of daily changes.

The direction and counsel of E. C. LaFond is gratefully acknowledged. Thanks are also due to the other members of the Physical Oceanography Section of Navy Electronics Laboratory for their assistance and advice.

OBSERVATIONAL TECHNIQUES

Samples of water for oxygen analysis were collected with a Fjarlie type bottle and processed immediately using the Winkler method. For a series of samples, the Rideal-Stewart modification of the Winkler method as described in "Standard Methods for the Examination of Water and Sewage," 9th ed., 1949, was used to determine any effect of other dissolved materials on the chemistry of the analysis. No significant difference between the results of the two methods was found so the standard Winkler was considered to be accurate for the lake even

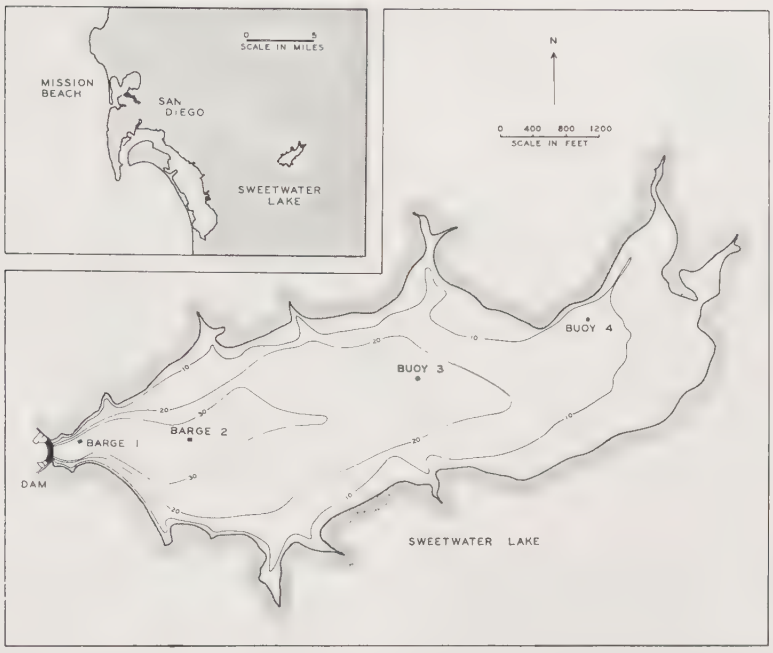

FIG. 1 Location of Sweetwater Lake. All data described were collected from Barge 2. Contours for lake depth are given in feet.

though the amount of dissolved organic matter was high.

Temperatures were measured with a thermistor type electronic thermometer which, with associated recording equipment, has ±0.1°F accuracy.

Serial observations were made from a barge anchored in the deeper part of the lake and were taken at 2 to 4 hour intervals continuously through four 30 to 48 hour periods beginning at about 0800 on 3, 4, and 5 April, 18 and 19 June, 2 and 3 July, and 16 and 17 July, 1957.

VERTICAL DISTRIBUTION OF OXYGEN

In spring, the oxygen content of Sweetwater Lake was found to diminish steadily with depth. However, marked stratification

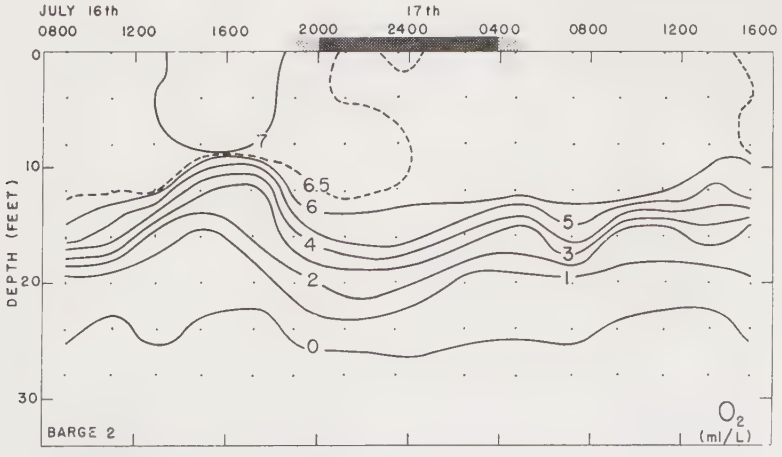

FIG. 2. Absolute concentration of oxygen in Sweetwater Lake for a 32 hour period in July. Dark band at top indicates hours of darkness.

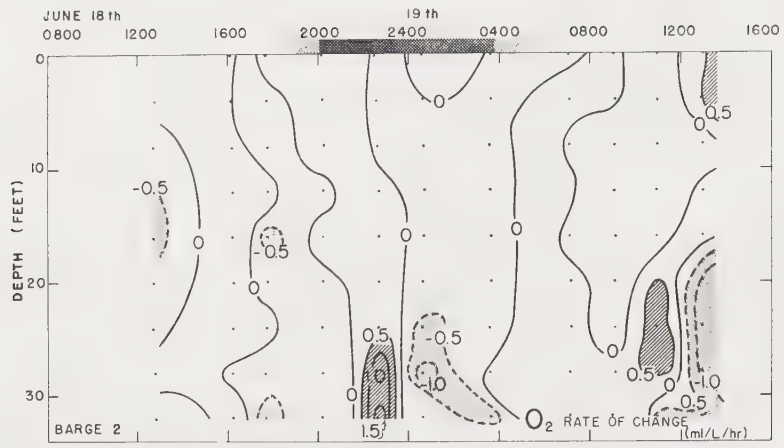

FIG. 3. Rate of change of oxygen concentration (expressed as ml/L oxygen increase or decrease per hour) on June 18–19.

appeared early in July and continued through August. The lake became divided into an upper oxygen-rich zone from 0 to 10 ft, a zone of rapid decrease in oxygen content from 10 to 25 ft, and a bottom layer of 2 to 5 ft in thickness which is devoid of oxygen (Fig. 2).

Each of the zones possesses certain characteristics which make it easily identifiable. The uppermost zone, extending from the surface to about 10 ft, is a region of uniformly high oxygen content of the order of 7 ml/L. Maximum oxygen values occurred in this region in the late afternoon with little other daily variation. Within the middle zone, from 10 to 25 ft, oxygen values ranged from 6 to less than 1 ml/L. This is a region of rapid decrease where the oxygen level may drop by 1 ml/L for every foot of increasing depth. Very rapid changes with time also occurred in these depths with rates of change on the order of 2 ml/L/hr observed in the late afternoon hours.

Close to the bottom at depths of 25 to 32 ft is the oxygen deficient layer typical of most deeper lakes during the summer stagnation period. In midsummer the oxygen content in this layer apparently only reaches detectable amounts when there is some downward excursion of water from higher levels. Usually no measurable oxygen is present.

FIG. 4. Rate of change of oxygen concentration (expressed as ml/L oxygen increase or decrease per hour) on July 2–3.

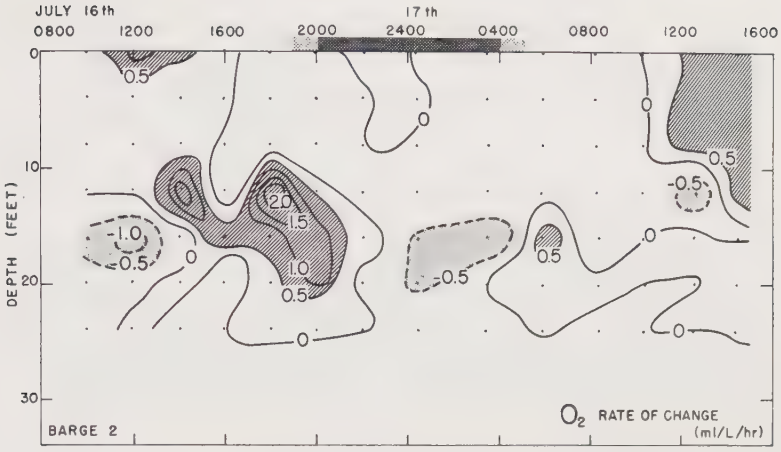

FIG. 5. Rate of change of oxygen concentration (expressed as ml/L oxygen increase or decrease per hour) on July 16–17.

CHANGES IN OXYGEN CONCENTRATION

Figures 3, 4, and 5 show the amount of change in oxygen (expressed in milliliters per liter per hour) for Sweetwater in June and July. The situation for late June and early July (Figs. 3 and 4) is indistinct, with little or no consistency of change at a given depth. This probably represents the unsettled conditions of spring with the summer pattern of circulation not yet established. By late July (Fig. 5) a pattern appears which seems to by typical for the summer.

One of the most interesting features of this summer pattern of oxygen change is the fact that the region of highest oxygen content is not the region of most marked oxygen change. The highest positive rates of change (indicating maximum oxygen increase) are found between 10 and 20 ft. This is probably best explained by circulation in the lake which seems to consist of rapid downwind surface flow with countercurrents at mid-depths in the region of the thermocline and oppositely flowing motions at lower depths produced by frictional drag. LaFond (1954) has previously described this mode of circulation for the lake, and it seems to agree very well with the observations made during the course of this study.

Circulation in the deeper parts of the lake was investigated by means of current drogues set at 2, 20 and 30 ft. Time-lapse

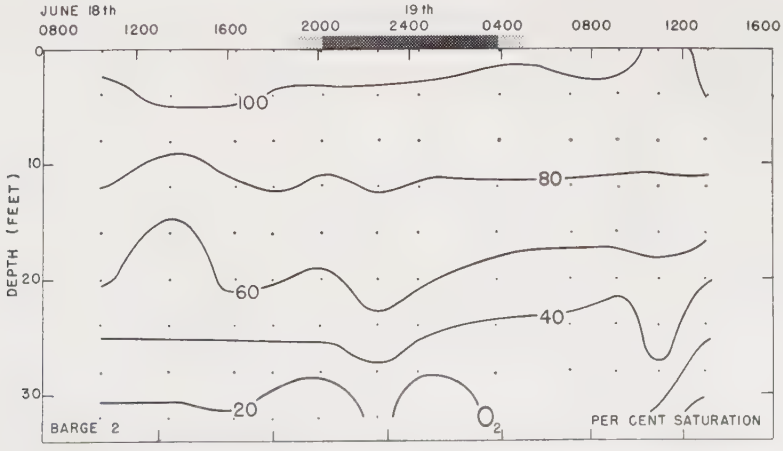

FIG. 6. Per cent saturation for oxygen in Sweetwater Lake on June 18–19.

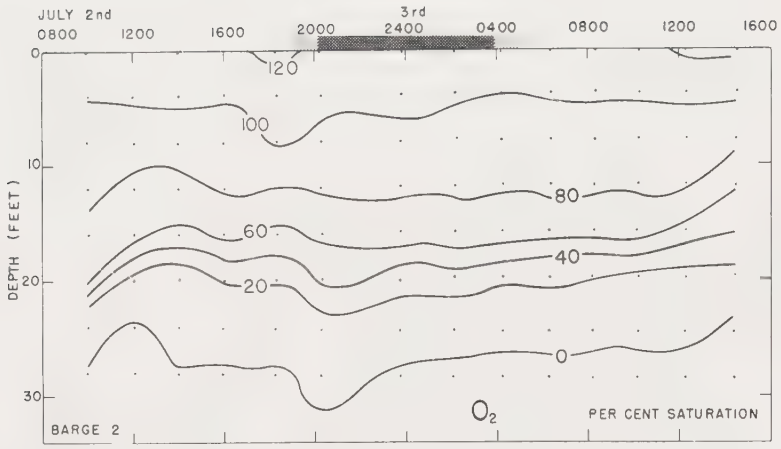

FIG. 7. Per cent saturation for oxygen in Sweetwater Lake on July 2–3.

motion pictures were made of movements of the drogues during a 10-hour period from 0800 to 1800. At 2 ft there was a rapid (estimated at 5 to 10 ft/min) downwind (easterly) movement with a wind velocity of 4 to 9 knots. At 20 ft movement was downwind but so slight that it could easily have been caused by wind action on the float marker, and at 30 ft the current was downwind at a speed of about ⅓ that of the near surface level.

Such relatively rapid circulation in the upper levels undoubtedly produces a horizontal and vertical current flow at mid-depths which would tend to separate the highly oxygenated water above from less oxygenated water below.

Another cause of the rapid decrease in oxygen with depth at mid-depths may be the presence of large populations of plankton at these depths as reported by Johnson (1949) and also found in the biological observations made concurrently with this study.

Oxygen saturations (see appendix) were calculated for all observations on Sweetwater (Figs. 6, 7, and 8). These show that supersaturation with oxygen occurs only within the upper few feet of the lake and seldom exceeds 120%.

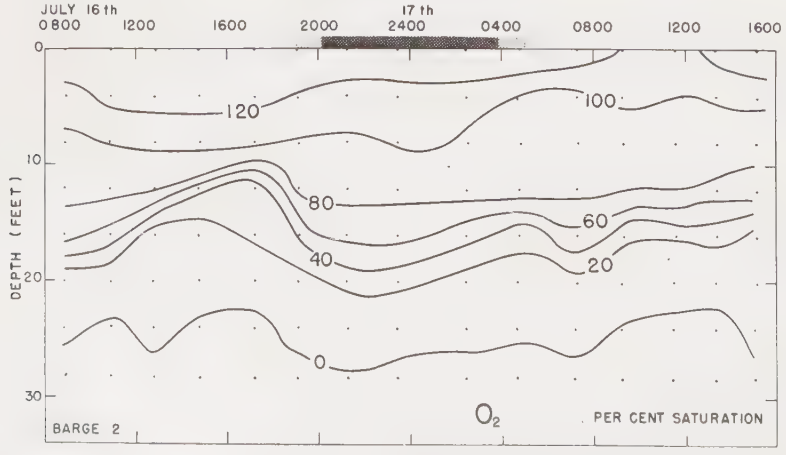

FIG. 8. Per cent saturation for oxygen in Sweetwater Lake on July 16–17.

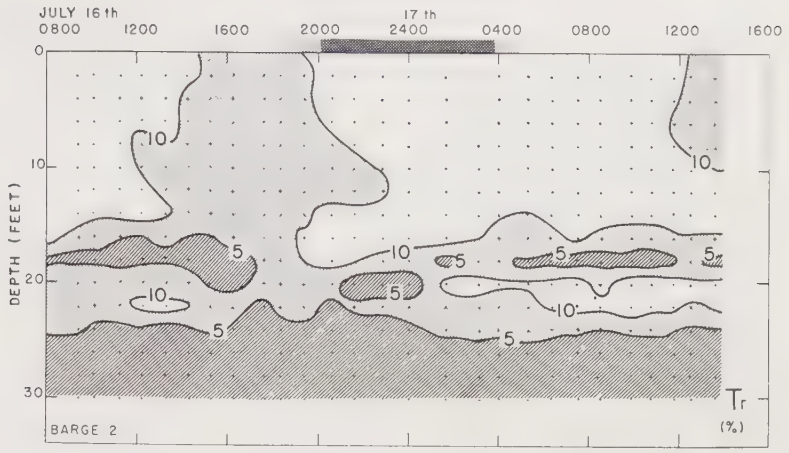

FIG. 9. Turbidity in the lake for July during the period corresponding to the time of oxygen measurement. Readings are given as per cent transparent with reference to air as 100%.

OBSERVED RELATIONSHIPS BETWEEN OXYGEN CONTENT AND OTHER HYDROGRAPHIC CONDITIONS

Turbidity

It might be expected that a definite correlation could be established between the amount of oxygen present in the water and turbidity, since those organisms largely responsible for production and use of oxygen would also tend to increase the turbidity. No such relationship was observed at Sweetwater. Figure 9 shows the turbidity for the same period and depths as the oxygen values shown in Figure 8. Turbidity measurements were made by means of a lamp projecting a beam over a distance of 1 meter to a photocell (hydrophotometer) mounted to be virtually free of ambient light. Readings are given as percentage of light transmitted (transparency) with reference to air as 100%.

A comparison of Figure 2 with Figure 9 shows that the water may be equally turbid near the bottom, where there is little or no oxygen, and near the surface where there is abundant oxygen. Rates of change for oxygen content for all observations also had no ascertainable connection with the turbidity. Absence of correlation between oxygen content and transparency of the water indicates that suspended inorganic particles must have produced the observed turbidity.

Temperature

The heat present in a mass of water exerts a profound influence upon all dissolved gases, there being an inverse relationship between the solubility of gases and temperature. For oxygen, under normal atmospheric pressure, the data of Truesdale *et al.* (1955) show that in fresh water a temperature change of 1°C in the 20–30°C range will inversely affect the solubility by about 0.05 ml/L. A 1°C change in the 10–20°C range will change the solubility about 0.1 ml/L, and in the 0–10°C range a 1°C change will change the solubility about 0.2 ml/L. Thus, if all other conditions are equal, cool water can be expected to contain more dissolved oxygen than warm water.

Figure 10 is a temperature-depth profile for Sweetwater in Mid-July illustrating the temperature situation usually found in the deeper part of the lake during the summer. Below 15 ft only minor fluctuations of temperature occur; above 15 ft the daily heating and cooling cycle is apparent.

Average temperature in the deeper part of the lake increased from 72.7°F on 18 and 19 June to 77.0°F on 16 and 17 July. This increase in temperature, sufficient to lower the solubility of oxygen by 0.12 ml/L, would produce higher saturation values at all depths if the oxygen content remained the same. However, the average oxygen level dropped from 5.13 ml/L in June to 3.26

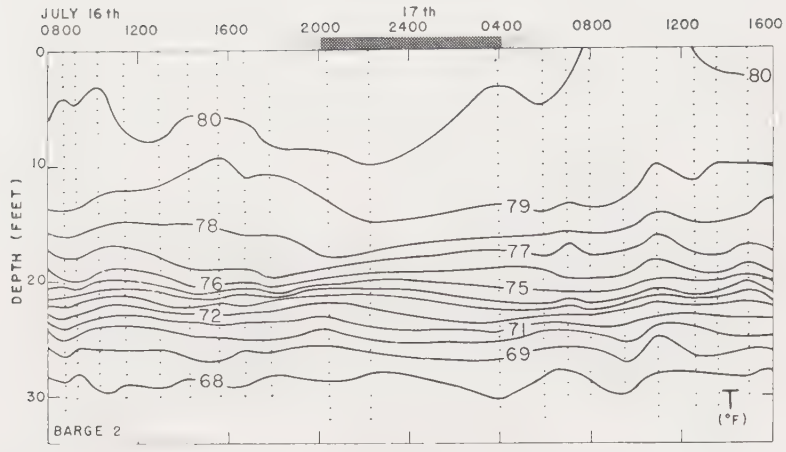

FIG. 10. Temperature-depth profile for the Lake in July.

ml/L in July. Actually, the decrease in July was entirely due to the virtual disappearance of oxygen at all depths below 16 ft. Above 16 ft, the average oxygen level during this period remained almost constant, increasing only from 6.28 ml/L in June to 6.33 ml/L in July. The average temperature in the upper 16 ft, however, increased from 75.0°F to 80.1°F. This raised the average saturation in the upper 16 ft of water from 87.5% in June to 93.4% in July. Saturations greater than 100% occurred only above an average depth between 2 and 3 ft in June, but in July 100% saturation occurred above an average depth between 5 and 6 ft.

As the summer progressed, the lake became more sharply divided into a layer of highly saturated or supersaturated water (above 16 ft deep) over an oxygen-depleted bottom layer. This situation is maintained because the warmer oxygen-rich water above, being less dense, cannot easily circulate downward to replace the oxygen-deficient water below. But thermal stratification and resultant two-part circulation did not seem sufficient to account entirely for the sudden accumulation of oxygen-depleted water at the lower depths which occurred between June and July. A more likely direct cause was the gathering of decomposing materials at the bottom which would remove dissolved oxygen at a faster rate than any downward excursion of oxygenated water from above could replace it. The large plankton blooms observed also probably contribute continuously to the decomposing materials at the bottom which would remove dissolved oxygen faster than it could be replaced from above. Hutchinson (1938) notes that oxygen deficient hypolimnia are characteristic of highly productive lakes.

Daily Changes

The oxygen content in any biologically productive body of water is influenced by daily changes in light intensity, since the oxygen producing photosynthetic activities of phytoplankton largely determine the oxygen content. This diurnal cycle in

TABLE 1. *Oxygen tension at the surface of Sweetwater Lake*

	18 and 19 June	2 and 3 July	16 and 17 July
Average value for P – p during period of observations	–0.024	–0.033	–0.037

Values computed by the equation

$$P - P = P(O_b - O_a)/O_b$$

where P is the partial pressure of oxygen in the atmosphere, p is the oxygen pressure in the water, O_a is the oxygen content of the water and O_b is the solubility of oxygen under the specified conditions. Negative values for P–p indicate that oxygen will pass from the water to the atmosphere.

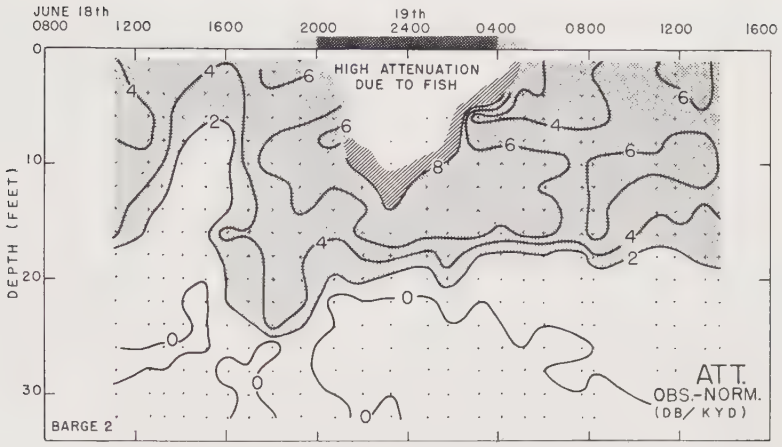

FIG. 11. Sound attenuation on 18 and 19 June. Values given are differences between observed and normal attenuation.

Sweetwater can be seen in Figure 2 where oxygen levels in the upper depths rise rapidly until sunset then drop to minimum in the early morning hours. Rate of change (Fig. 5) also reflects the daily cycle particularly in the zero line (compensation point), which rises to the surface at nightfall and sinks during daylight.

Evaluation of the equation used by Redfield (1948) to measure oxygen exchange across the air-water interface (Table 1) gives almost exclusively negative values, indicating that oxygen will tend to pass from the water to the air at this season. This would rule out the possibility that the upper layers in the lake become well-oxygenated by taking on atmospheric oxygen, and suggests that the high oxygen levels in the lake at this time come entirely from biological activity.

Acoustical Properties

Sound velocity and attenuation were measured concurrently with the oxygen in an effort to relate changes in the acoustic environment with biological activity as indicated by the oxygen content. Since Greenspan and Tschiegg (1956) have reported that concentrations of dissolved air ranging from a few per cent to saturation have a negligible effect on sound velocity, it was not expected that there would be a direct correlation between amounts of dissolved oxygen and acoustic conditions.

Sound velocity was measured with a NBS-ONR Underwater Velocimeter, and differences between the observed and theoretical velocities for the observed temperature and pressure were calculated. The resulting values were found to be very close to the limits of error for the velocimeter making these data inconclusive.

Sound attenuation was measured with a resonant cavity designed by W. J. Toulis of the Navy Electronics Laboratory. Figure 11 shows the anomalies in attenuation for 18 and 19 June at Sweetwater. Values shown are differences between observed and theoretical for the observed temperature and pressure. Attenuation data for this date are representative for that encountered for all the observations. The only apparent relationship shared between the level of dissolved oxygen and degree of attenuation of sound is the general decrease of both with depth.

APPENDIX

Method of calculating oxygen saturation

Expression of oxygen concentration as per cent saturation is a convenient method often used in oceanography and limnology for stating the relation between observed values for oxygen and the amount which could be dissolved at the temperature of the observa-

tion. Usually, per cent saturation is found by

$$\frac{O_a}{O_b} \times 100 = \% \text{ saturation}$$

where

O_a = measured oxygen content of the water

O_b = solubility of oxygen in the water at the observed temperature and salinity when in equilibrium with a standard atmosphere having a total pressure of 760 mm.

Although it appears to be a simple and straightforward calculation, the expression of oxygen saturation is often misleading since the solubility (O_b) is not used consistently. At a given depth, the solubility of a gas cannot be considered to be the same as the value when in equilibrium with normal atmospheric pressure since hydrostatic pressure must also be taken into account. The following brief discussion is presented here in order to make clear the meaning of per cent saturation as used in this study.

Miyake (1951) has proposed the term "saturation amount *in situ*" for the solubility corrected for increased pressure with depth and "saturation percentage *in situ*" for the per cent saturation calculated using the corrected solubilities. Saturation amount *in situ* is found by:

Sat. amount *in situ* = Pressure *in situ* × Normal sat. amount, where pressure *in situ* is the sum of the hydrostatic pressure and atmospheric pressure in atmospheres.

For the purposes of this study, Miyake's idea was used and oxygen saturations were calculated by the following formula:

$$S_a = \frac{O_a}{O_b \times p/760} \times 100$$

where

S_a = per cent saturation

O_a = observed concentration of oxygen in ml/L

O_b = solubility of oxygen from the air (in ml/L) at observed temperature and standard pressure of 760 mm.

p = hydrostatic pressure for depth of sample (in mm.)

It should be noted that oxygen saturations calculated in this way do not represent absolute oxygen saturations. The increasing solubility of oxygen in water of a given temperature as depth increases is actually greater than the increase in pressure alone would indicate. Since the amount of dissolved nitrogen remains constant, the relative amounts of other gases capable of being dissolved is considerably increased. Absolute oxygen saturations may be calculated from a formula given by Ricker (1934) which takes into consideration the relative decrease in amount of dissolved nitrogen with increasing depth.

It should also be noted that the value of O_b must be corrected for samples taken at higher elevations or when deviations from 760 mm atmospheric pressure become significant. Since the elevation of Sweetwater is only about 200 feet above sea level, no correction for altitude was used in calculating oxygen saturations.

REFERENCES

Am. Pub. Health Assoc. 1946. "Standard methods for the examination of water and sewage." 9th ed., New York, 286 pp.

Greenspan, M., and C. E. Tschiegg. 1956. The effect of dissolved air on the speed of sound in water. J. Acoustical Soc. Am., **28**(3): 501.

Hutchinson, G. E. 1938. On the relation between the oxygen deficit and the production and typology of lakes. Int. Rev. Hydrobiol., **36**: 336–355.

Johnson, Martin W. 1949. Relation of plankton to hydrographic conditions in Sweetwater Lake. J. Am. Water Works Assoc., **41**(4): 347–356.

LaFond, E. C. 1954. Factors affecting temperature gradients in the upper layers of the sea. Sci. Monthly, **38**(4): 69–76.

McEwen, G. F. 1941. Observations on temperature, hydrogen ion concentration and periods of stagnation and overturning in lakes and reservoirs of San Diego County, California. Bull. Scripps Inst. Oceanog., **4**(9): 219.

Miyake, Y. 1951. The possibility and allowable limit of formation of air bubbles in the sea. Pap. Met. Geophysics, **2**(1): 92–101.

Redfield, A. C. 1948. The exchange of oxygen across the sea surface. J. Mar. Res., **3**: 347–361.

Ricker, W. E. 1934. A critical discussion of various measures of oxygen saturation in lakes. Ecology, **15**: 348–363.

Truesdale, G. E., A. L. Downing, and G. F. Lowden. 1955. The solubility of oxygen in pure water and sea water. J. Appl. Chem., **5**(2): 53–62.

THE RESISTANCE OF MARINE ZOOPLANKTON OF THE CARIBBEAN AND SOUTH ATLANTIC TO CHANGES IN SALINITY[1]

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ABSTRACT

It is generally assumed that plankton of the open seas—regions which exhibit relatively constant high salinities—are stenohaline. This paper reports a preliminary investigation of the tolerance of Caribbean and and South Atlantic marine zooplankton to both increases and decreases in salinity. The majority of forms studied will withstand salinity changes much greater than they would be expected to encounter in their normal environment, thus suggesting that salinity may not be a limiting factor in their distribution. The forms studied are listed in the order of their ability to resist salinity change.

INTRODUCTION

On the basis of their ability to withstand salinity changes, animals are generally classified as stenohaline or euryhaline, and it is usually assumed that planktonic forms of the open sea—regions which normally have relatively constant high salinities—are stenohaline. Evidence for his is based mainly on distribution studies in relation to salinity determinations.

Although there have been investigations of salinity tolerances of marine organisms (Pearse 1928, Beadle 1931, Barnes 1932, Nagel 1934, Sayles 1935, Topping and Fuller 1942), these have dealt mostly with larger forms living in the relatively low-salinity waters near the coastline. As far as this investigator is aware, there has been no experimental work on the salinity tolerances of marine zooplankton.

METHODS

During the summer of 1957 aboard the Lamont Geological Observatory R/V VEMA, salinity tolerances of a number of planktonic animals of the Caribbean and South Atlantic waters were determined. Zooplankton, caught in routine plankton tows, were placed in plastic dishes containing 200 ml of sea water, which was then diluted by various amounts of distilled water. In early experiments the water was aerated. However, there was no significant decrease in oxygen content in aerated and non-aerated jars over the length of time the experiments were conducted, nor was there any difference in mortality of plankton in aerated and non-aerated jars. Artificial aeration was therefore not used in the majority of the experiments. It was not possible to maintain constant temperatures, and no effort was made to control temperature, other than protecting the culture dishes from the direct sunlight. Controls were animals of the same species kept in 200 ml of sea water collected at the time the tow was made. A number of experiments on tolerance to increased salinities were made by adding various amounts of high salinity water to normal sea water. High salinity water was obtained by boiling sea water. It is recognized that the possibility exists that in the process of boiling sea water variables other than salinity may be changed such as modification of organic content, changes in ionic balance, etc. Salinities of all waters in which the animals were raised were determined at the conclusion of each experiment by the Mohr silver nitrate titration method.

Survival time in water of different salinities was compared to survival time in normal sea water. Where it was possible to use large numbers of animals of the same species, the time to death of one-half the original number (LD-50) was used. Survival times were compared among forms from the following groups: Hydrozoa, Poly-

[1] This project was supported by a research grant from the Lalor Foundation. The author wishes to express his appreciation to Dr. Maurice Ewing, Director of the Lamont Geological Observatory for granting to him the facilities of the R/V VEMA during the course of this investigation.

chaeta, Copepoda, Cirrepedia, Amphipoda, Decapoda, and Tunicata.

RESULTS

Survival time of controls

There was a marked difference in survival times of controls of different species. Those animals that were difficult to keep alive were: hydrozoan medusae, 1–1½ hours; Tunicata (salps), 1–1½ hours; Euphausiacea, 3½–4 hours; *Sagitta*, 4–6 hours. Controls of all other forms survived longer than 10 hours.

Tolerance to decreased salinities

1. Hydrozoan medusae, salps, euphausiids.—In those forms in which the controls lived less than 2 hours the experimental animals died at approximately the same time, and no comparisons on tolerances could be made (medusae, salps). In the 3 experiments in which *Euphausia pelagica* was studied, dilutions of 4% (change of salinity from 36.60‰ to 35.10‰ in one case and comparable changes in the others) resulted in the death of all the euphausiids in 3 hours, while the controls lived for 4 hours. Dilutions of 15% and over cut the survival times in half. There is some question whether or not any valid conclusion can be drawn from these experiments, but the much more rapid deaths of the animals, even in solutions of low dilution, would indicate that these forms may well be classified as stenohaline.

2. Brachyuran larval forms.—Zooea and megalopa larvae in the 4 experiments in which they were included were never killed by any dilutions used and outlived all other forms included in the same experiments (*Lucifer*, annelids, amphipods, copepods). The highest dilution to which they were subjected was 22%, and the larvae lived for more than 20 hours in this low-salinity water (28.69‰; control salinity, 36.60‰). No difference was observed between the zooea and the megalopa stages.

3. Barnacles.—Two experiments were conducted using the barnacle, *Lepas*, removed from floating Sargassum weed. In both experiments, the barnacles lived for more than 30 hours in 50% dilutions (salinity, 20.32‰). They were observed to be open periodically during the time of the experiment.

4. Natantia.—Two species, *Palaemon natator* and *Latreutus ensiferus*, of this decapod suborder were tested in one experiment. These animals were also removed from Sargassum weed. At the termination of the experiment after 20 hours all of the animals were still alive in both control and experimental dishes. Salinities down to 29.67‰ (19% dilution) were the lowest to which they were exposed.

5. *Lucifer*.—Animals in this genus, also belonging to the decapod suborder Natantia, were the subject of the 4 experiments and were exposed to 3, 5, 10, 13, 14, 15, and 17% dilutions. In all experiments the animals in diluted water survived as long as the controls. (Lowest salinity, 29.64‰ for 17 hours.)

6. *Sagitta*.—In five experiments involving the arrow-worm, animals exposed to dilutions up to 18% (salinity, 28.69‰) lived as long as the controls, 4–6 hours. Exposure to higher dilutions, 30–40%, cut the survival time in half.

7. Annelids.—Marine polychaets were tested in 2 experiments. They were in dishes in which copepods, amphipods, and *Lucifer* were also included. The annelids survived until the end of the experiments at which time all other forms but *Lucifer* had died (17 hours at 17% dilution). Dilutions of 25% killed all the annelids in 4 hours.

8. Amphipods.—Amphipods were included in 9 experiments. The forms tested included: *Phronima atlantica*, *Oxycephalus porcellus*, *Brachyscelus* sp., *Tryphana* sp., *Hyperia* sp., and 2 unidentified species from the family Gammaridae. Only in dilutions in excess of 15% was there any difference in survival times of experimentals and controls, and even in 20% dilutions some individuals (2 out of 3 in one instance) survived until the end of the experiment.

9. Copepods. — Seventeen experiments included copepods. Since they were present in abundance, it was usually possible to compare LD-50 survival times in most cases. Figure 1 shows the LD-50 survival times in the different dilutions. The average

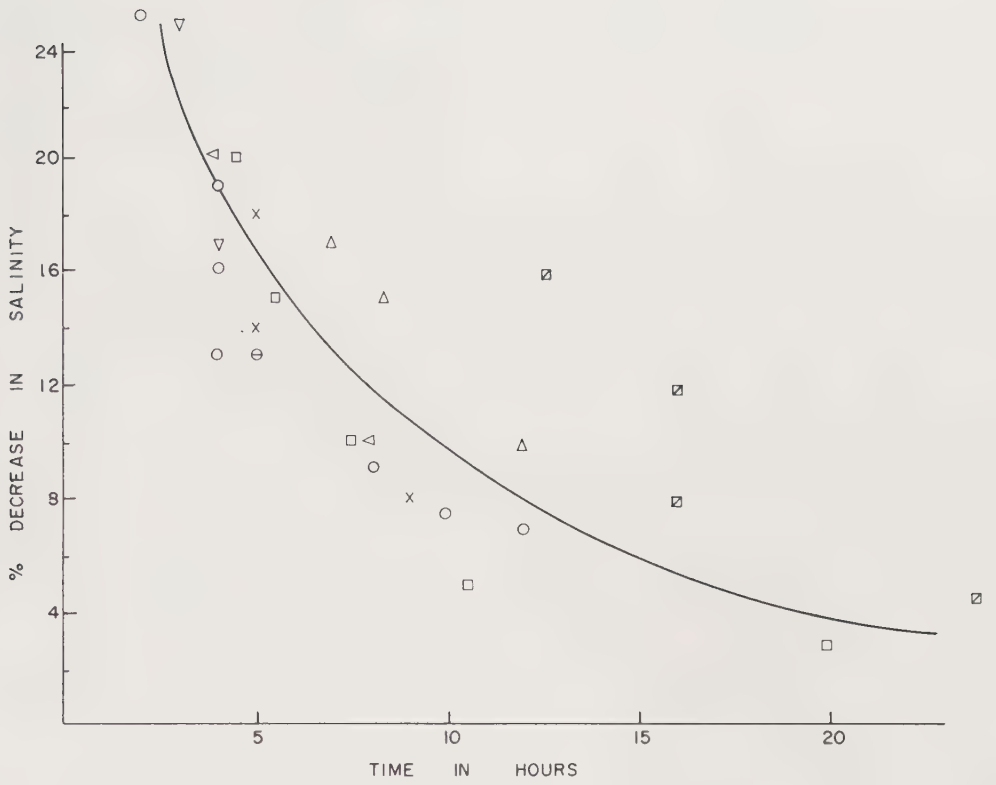

FIG. 1. The effect of decreased salinity on the LD-50 survival time of marine copepods. Each symbol represents a different experiment, *i.e.*, survival time in different salinities of animals obtained from a single haul. In most cases each experiment included a number of different species.

survival time of the controls in these same experiments was 14 hours, and by reference to this graph it is apparent that dilutions up to approximately 7% were without effect on survival. This dilution represents an average salinity of about 33.50‰—a salinity lower than is normally encountered in the open ocean. The species used in these experiments included *Undinula vulgaris, Eucalanus attenuatus, Candace pachydactyla, Pleuromamma xiphias, Labidocera acutifrons, Temora dubia, Scolecithrix danae, and Euchaeta* sp., from the suborder Calanoida; and *Copelia mirabilis, Saphirina stylifera, S. auronitens, Oncaea venusta,* and *Corycaeus obtusus* from the suborder Cyclopoida.

There was no noticeable difference between species with the exception of the 2 species of *Saphirina,* which appeared to be more tolerant than any other form to both increased and decreased salinities.

Tolerance to increased salinities

A number of experiments were conducted using increased salinities. In all of these, survival times were considerably shorter than those for corresponding decreased salinities. Amphipods, on which decreased salinities of 15% had no effect on survival time, lived less than half the length of time of controls when the salinity was increased by only 5% (salinity 38.71‰). A 10% increase in salinity, to 40.21‰ in one experiment, gave a survival time of 2½ hours as compared to more than 14 hours for the controls.

Among the copepods for which a 20% decrease in salinity resulted in the death of all animals in 7 hours, a 20% increase (salinity 43.00‰) killed all the animals in 3 hours. Figure 2 shows the results of the experiments on copepods. Comparison with Figure 1 shows the much more marked ef-

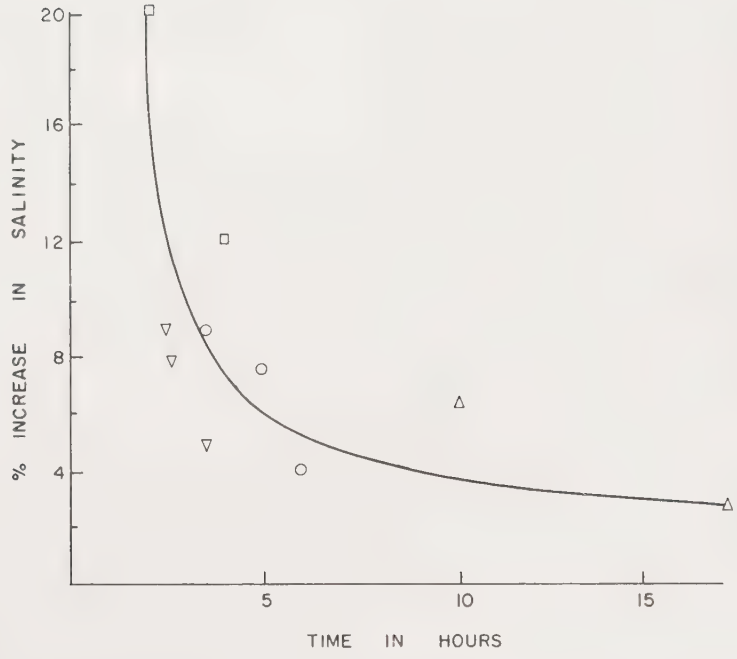

FIG. 2. The effect of increased salinity on the LD-50 survival time of copepods. Each symbol represents a different experiment. The LD-50 survival time of controls averaged 11 hours.

fect of increased salinity on survival time. The use of boiled sea water and the possibility of modification of factors other than salinity may account for these differences.

DISCUSSION

Listing the forms studied in the order of decreasing resistance to salinity changes summarizes the above results:

Form	Maximum % salinity change allowing survival time as long as controls
Barnacle	−50 to ?
Brachyuran larvae	−20 to +20
Natantia	−20 to +15
Natantia (*Lucifer*)	−20 to ?
Annelida	−20 to +8
Sagitta	−1-8 to +3
Amphipoda	−15 to +5
Copepoda	−7 to +5
Euphausiacea	−2 to +2
Hydrozoan medusae	—
Tunicata	—

All the forms studied down through the Copepoda will withstand salinity changes much greater than they would be expected to encounter in their normal environment of the open ocean. The data would thus suggest that salinity is not a limiting factor in the distribution of these forms. However, although the animals studied in these experiments survived under the conditions of the experiment as long as their controls, additional studies on growth and reproduction at different salinities would have to be made to confirm this probability.

The data are certainly scanty in many respects and cannot be taken to represent anything more than a preliminary and general survey of the problem. Although they show that there are 12 species from 2 suborders which can withstand 7% dilutions without any effect on survival time, within the large group of copepods there are undoubtedly some forms more resistant than others. On the basis of 2 experiments with 2 different species of marine polychaets it is, of course, not warranted to conclude that marine annelids as a group are highly resistant to salinity changes. Rather marked differences in survival times, respiratory rates, and volume changes in response to decreased salinities within the single genus *Nereis* have been reported previously (Beadle 1931, Sayles 1935). However, the

high tolerance of the few annelids examined would indicate that further studies along these lines are justified. Although these general statements could be made for all of the forms studied, the experiments indicate that salinity tolerances in certain forms may be somewhat higher than expected in animals from the open ocean and particularly from the high-salinity area investigated here. Continued investigation of this problem, with concentration on specific groups, should yield more conclusive results.

Certainly, salinity tolerances as studied in these experiments do not support definite conclusions as to whether or not salinity is a limiting factor in the distribution of the forms examined. But neither does a correlation between known distribution and measured salinity give the answer. Rather, a more complete analysis of the effect of salinity changes on all phases of the life history of each group must be made before any definite conclusions are drawn.

REFERENCES

Barnes, T. C. 1932. Salt requirements and space orientation of the littoral isopod, Ligia, in Bermuda. Biol. Bull., **63**: 296–504.

Beadle, L. C. 1931. The effect of salinity changes on the water content and respiration of marine invertebrates. J. Exp. Biol., **8**: 211–227.

Nagel, H. 1934. Osmoregulation in Crustacea. Ztschr. Vergl. Physiol., **21**: 468–491.

Pearse, A. S. 1928. On the ability of certain marine invertebrates to live in diluted sea water. Biol. Bull., **54**: 405–409.

Sayles, L. P. 1935. The effects of salinity changes on body weight and survival of *Nereis virens*. Biol. Bull., **69**: 233–240.

Topping, F. L., and J. L. Fuller. 1942. The accommodation of some marine invertebrates to reduced osmotic pressure. Biol. Bull., **82**: 372–384.

WATER QUALITY AND UPWELLING AT GRAYS HARBOR ENTRANCE

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ABSTRACT

The incoming ocean water entering Grays Harbor, Washington on flood tide was observed periodically to contain abnormally low dissolved oxygen concentrations. Low dissolved oxygen concentrations ($\leqslant$5.0 mg/L or 3.5 ml/L) were associated generally with significantly lower than normal ocean water temperatures which presumably results from upwelling along the coast. On a given tidal cycle the oxygen deficiency from normally assumed saturation levels for ocean water is equivalent to the oxygen demand associated with the domestic sewage discharge of 20 million persons. It appears that upwelling phenomena may negate conclusions based on oxygen balances in pollutional analyses of estuaries unless the actual dissolved oxygen concentration at the ocean source is determined.

INTRODUCTION

The periodic occurrence of upwelling of relatively deep ocean waters upon the Pacific coastal shelf has been recognized for many years (Sverdrup *et al.* 1956, Sverdrup 1938, and Stevenson and Gorsline 1956). For the most part oceanographers have been concerned with the physical causes of upwelling as related to prevailing winds, density layers in the sea, and internal waves of large amplitude and period (Stevenson and Gorsline 1956, Hidaka 1954, and Saito 1956). Relatively little attention has been given to the physical, chemical, and biological characteristics of upwelled water masses and their effect on the coastal environment. Of particular interest is the effect of upwelling on the dissolved oxygen characteristics of coastal and estuarial waters.

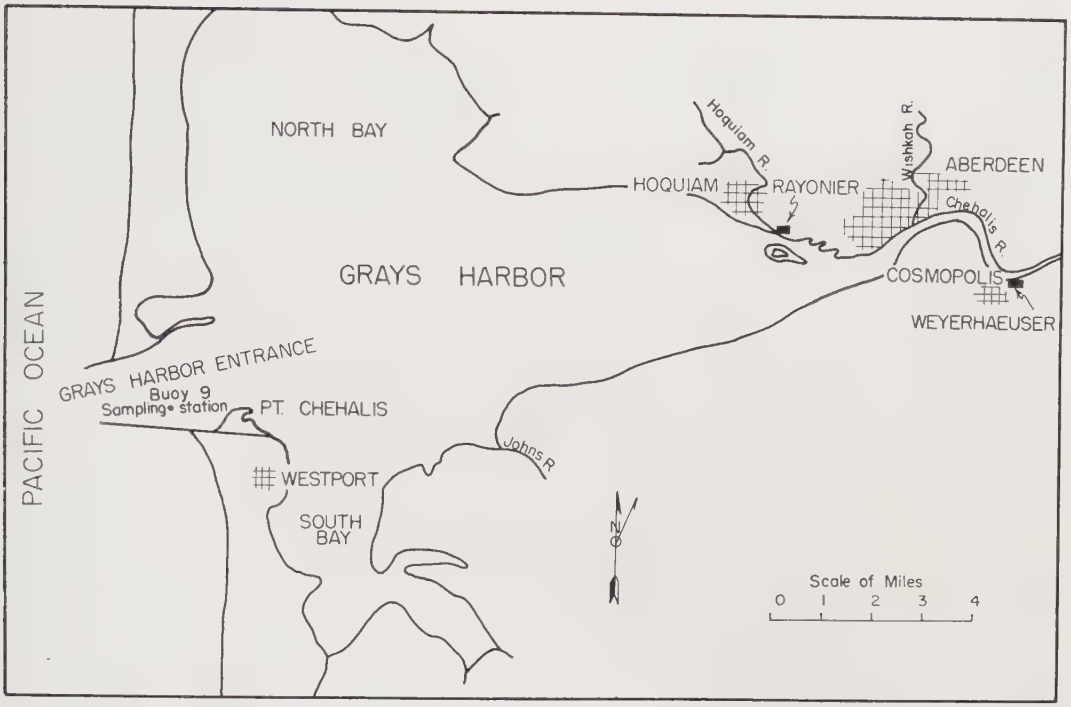
Rayonier Incorporated, which produces dissolving pulp at their Grays Harbor Division plant in Hoquiam, Washington, has conducted water quality surveys of Grays Harbor for many years. The objectives of these surveys include the development of quantitative information about the general condition of the water throughout the estuary and the development of basic data related to the design and operation of the plant's waste disposal facilities.

An outline map of the Grays Harbor estuary showing the general shape of the estuary, its size, type of ocean entrance, location of sampling stations, as well as the location of the Rayonier and Weyerhaeuser pulp mills is presented in Figure 1.

THE RAYONIER PROGRAM

In 1950 an expanded program of investigation of Grays Harbor was initiated in order to define the relationship between the Rayonier plant waste discharge and the water quality characteristics of the harbor. Of primary concern was the correlation of dissolved oxygen concentrations in the harbor with known waste discharge quantities and characteristics. The principal waste discharges to Grays Harbor at that time appeared to be the Rayonier plant waste, wastes from several other industries such as slaughterhouse and meat processing plants, fish and shellfish freezing and canning establishments, other canneries, several lumber operations, and the untreated domestic sewage from the cities of Aberdeen, Cosmopolis, and Hoquiam.

Waste concentrations in the harbor resulting from pulping operations were monitored with reasonable precision by means of the modified Pearl-Benson method for spent sulfite liquor. Extensive efforts, involving thousands of analyses, to correlate the discharge of known wastes and the concentrations of wastes in the harbor with observed dissolved oxygen concentration were unsuccessful, indicating the presence of a significant but unknown variable. Accordingly, systematic analyses were undertaken above the effect of tidewater of all streams and tributaries entering Grays Harbor as well as of the incoming ocean water at Grays Harbor entrance. No unusual water quality



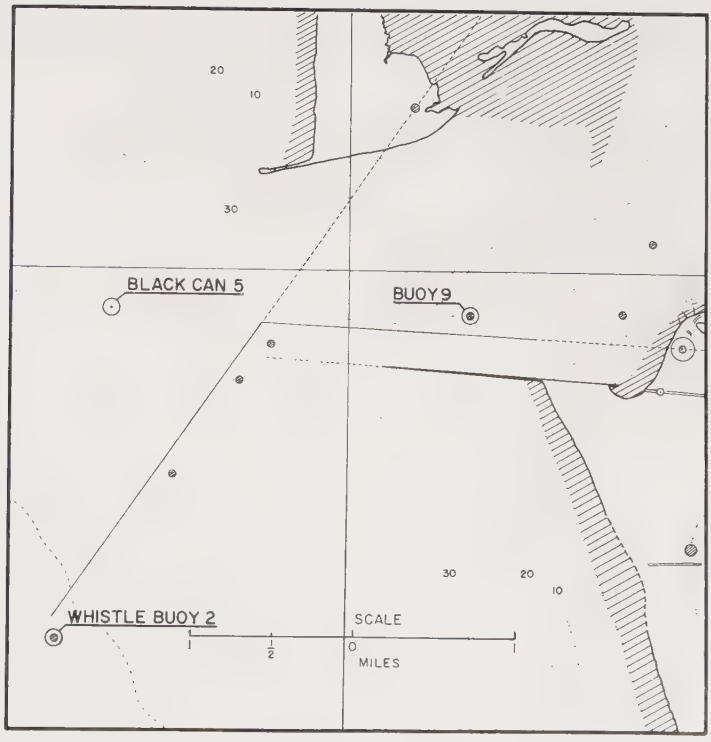


FIG. 1. Grays Harbor, Washington.

characteristics were noted in any of the tributary streams. However, on the first sampling trip to Grays Harbor entrance on September 13, 1950, samples of water taken off Point Chehalis approximately three hours after low tide showed dissolved oxygen concentrations far less than the expected saturation or near-saturation levels. From the surface to bottom, the dissolved oxygen concentration was less than 5.0 mg/L (3.5 ml/L) and averaged 4.5 mg/L (3.1 ml/L). Samples taken at Buoy 9 and other locations in the proximity of Point Chehalis indicated that the oxygen deficient water was not limited to a small isolated area but was characteristic of the general ocean water mass in the vicinity of the harbor entrance.

The following day, September 14, 1950, a check sampling trip to the same stations and at the same tidal condition showed average dissolved oxygen concentrations varying from 7.5 to 8.0 mg/L (5.2 to 5.6 ml/L) indicating a transient phenomenon requiring further investigation. Subsequent sampling trips in the vicinity of Buoy 9 and on flood tide on September 16 and 18, 1950, yielded numerous water samples having less than 5.0 mg/L (3.5 ml/L) of dissolved oxygen with more than 80% of the samples containing less than 6.0 mg/L (4.2 ml/L) of dissolved oxygen.

Because of the importance of the dissolved oxygen content of the incoming ocean water as related to the level of oxygen concentrations within the harbor, a fairly extensive program for monitoring the incoming ocean water has been conducted since 1950. Each year at least six monitoring trips have been made covering the area from Hoquiam to Grays Harbor entrance (Buoy 9). For practical reasons and to suit time restrictions, the monitoring at Buoy 9 was limited to a series of samples taken at three depths (3 ft, 15 ft, and approximately 5 ft from bottom) at one half-hour intervals for four hours commencing approximately one hour after low tide. Such a series should give a representative sample of the characteristics of the ocean water entering the harbor during a particular flood tide.

RESULTS

Dissolved oxygen characteristics

Figure 2 presents the dissolved oxygen characteristics of the incoming ocean water on six different days when significant amounts of oxygen deficient ocean water were observed. While the lowest oxygen level recorded was 2.3 mg/L (1.6 ml/L) in the bottom sample on July 27, 1956, and was nearly as low on August 20, 1951, it should be noted that the average oxygen concentration of the incoming water on August 22, 1951, was 4.0 mg/L (2.8 ml/L) or less for at least 2½ hours during the period of maximum flood.

It is of interest to note that the water characteristics appear to reflect essentially two different hydraulic conditions. One condition, as for example July 27, 1956, was characterized by oxygen deficient, apparently upwelled, water occurring immediately in advance of flood tide. The incoming water was of uniform dissolved oxygen concentration from the surface to bottom regardless of the level of oxygen deficiency. Apparently there had not been sufficient time for atmospheric diffusion of oxygen into the surface layers and downward transport of oxygen establishing an oxygen gradient prior to transport of the water mass into the harbor. Figure 2 also indicates a relationship between the "old" water returning to the harbor, and the "new" water not previously in the harbor. The increase in oxygen deficiency with length of time after low slack tide indicates the increasing influence of the "new" as compared with the "old" water entering the harbor.

The second condition, as evidenced by data reported for August 30, 1957, indicates either that oxygen deficient water had appeared sometime in advance of flood tide so affording time for diffusion of oxygen into the surface layers, or that oxygen deficient water appeared during flooding and did not mix with the shelf water but progressed into the harbor as a density layer or "finger" without any significant mixing.

It is also interesting to note that for a full one-hour period during maximum flood on July 27, 1956, the average dissolved oxygen

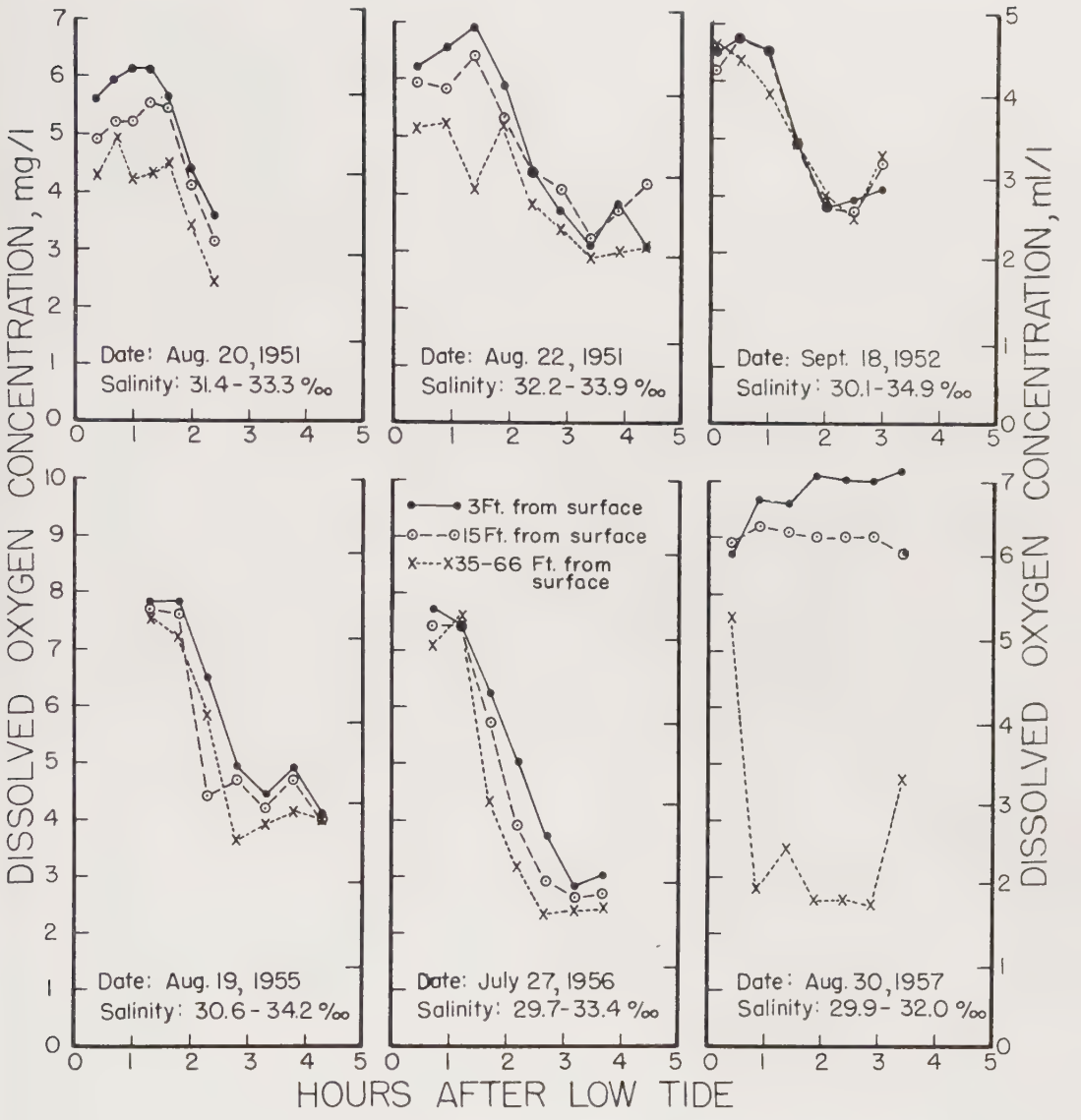

DISSOLVED OXYGEN CONCENTRATION, mg/l
DISSOLVED OXYGEN CONCENTRATION, ml/l
HOURS AFTER LOW TIDE
Date: Aug. 20, 1951
Salinity: 31.4 - 33.3 ‰
Date: Aug. 22, 1951
Salinity: 32.2 - 33.9 ‰
Date: Sept. 18, 1952
Salinity: 30.1 - 34.9 ‰
3Ft. from surface
15Ft. from surface
35-66 Ft. from surface
Date: Aug. 19, 1955
Salinity: 30.6 - 34.2 ‰
Date: July 27, 1956
Salinity: 29.7 - 33.4 ‰
Date: Aug. 30, 1957
Salinity: 29.9 - 32.0 ‰

FIG. 2. Dissolved oxygen characteristics of incoming ocean water, Grays Harbor entrance, Buoy 9.

concentration for the entire water mass at Buoy 9 was less than 3.0 mg/L (2.1 ml/L). On other days dissolved oxygen levels as low as 2.0 mg/L (1.4 ml/L) were observed while frequent samples contained less than 3.0 mg/L (2.1 ml/L).

The salinity of the incoming ocean water ranged from a minimum of 29.7‰; to a maximum of 34.9‰; the maximum value was observed near or at the end of each monitoring series indicating essentially 100% ocean water. Indicated spent sulfite liquor (S.S.L.) analyses were conducted on all samples and the observed values ranged from 0 to 3.0 mg/L of 10% S.S.L. (essentially natural background levels) in the oxygen deficient samples. These data confirm the assumption that the abnormal dissolved oxygen concentrations of the incoming water were a characteristic of the oceanic environment rather than a result of man's activities or waste discharge.

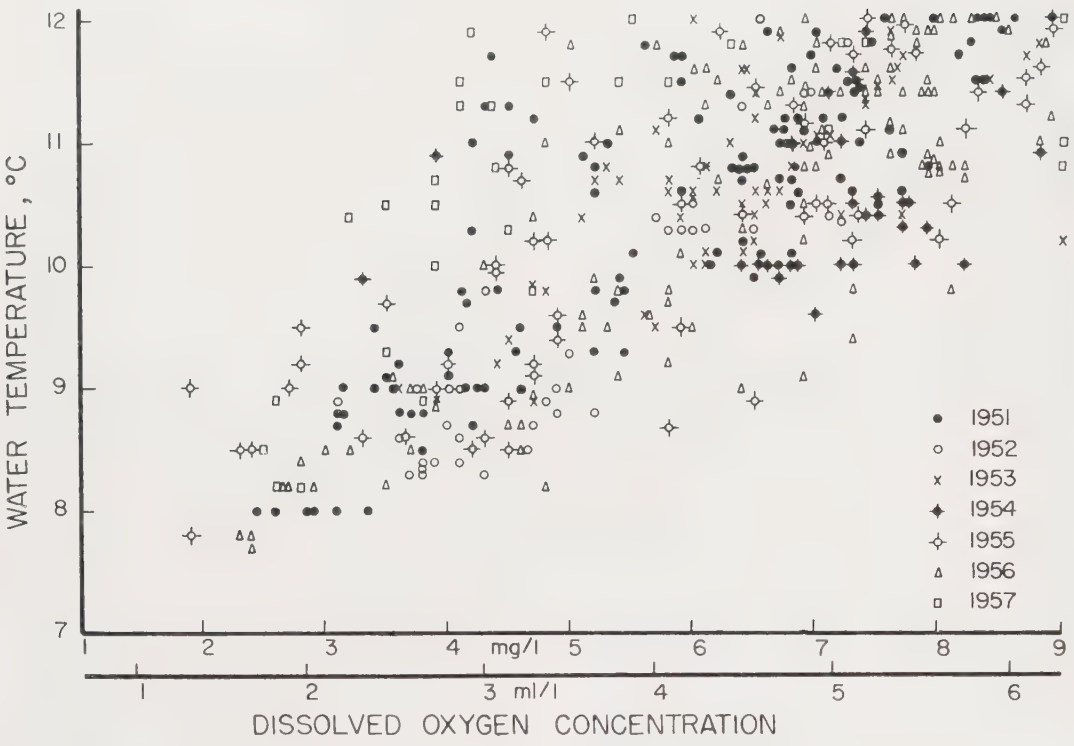


FIG. 3. Temperature-dissolved oxygen relationships of incoming ocean water, Grays Harbor entrance, Buoy 9, 1951–1957.

Dissolved oxygen-temperature relationships

Numerous water quality characteristics in addition to D.O., such as pH, alkalinity, biochemical oxygen demand (B.O.D.), indicated S.S.L., plankton, temperature, and chlorinity were determined on the incoming ocean water. However, the only significant relationship exhibited by the data was that between the temperature and dissolved oxygen level of the incoming water. In Figure 3 temperature is plotted against dissolved oxygen concentration for all water samples at Buoy 9 with a temperature equal to or less than 12°C for the years 1951 through 1957. While a high degree of correlation does not exist, there appears to be a distinct trend or relationship; of the 142 samples having temperatures less than 10°C, 109 or 77% contained dissolved oxygen concentrations of less than 5.0 mg/L (3.5 ml/L) and 44% less than 4.0 mg/L (2.8 ml/L). Similarly, all water samples with temperatures equal to or less than 8°C contained dissolved oxygen concentrations less than 3.5 mg/L (2.4 ml/L). Invariably, the lowest dissolved oxygen concentrations were associated with the coldest water.

Figure 4 gives the temperature and dissolved oxygen in samples taken at Grays Harbor entrance for two series of consecutive sampling surveys in 1956. These data show the gross and relatively rapid change in water temperatures and dissolved oxygen concentrations in the entering ocean water. It appears that the only rational explanation of the sudden drop in both water temperature and dissolved oxygen concentration is that it is the result of upwelling of the denser, cooler, oxygen deficient ocean waters on the coastal shelf. The decrease in temperature as flooding proceeded on July 20 without a generally associated dissolved oxygen concentration decrease was indicative of the increasing effect of colder "new" ocean water as the "old" harbor water was displaced. It should be noted, however, that

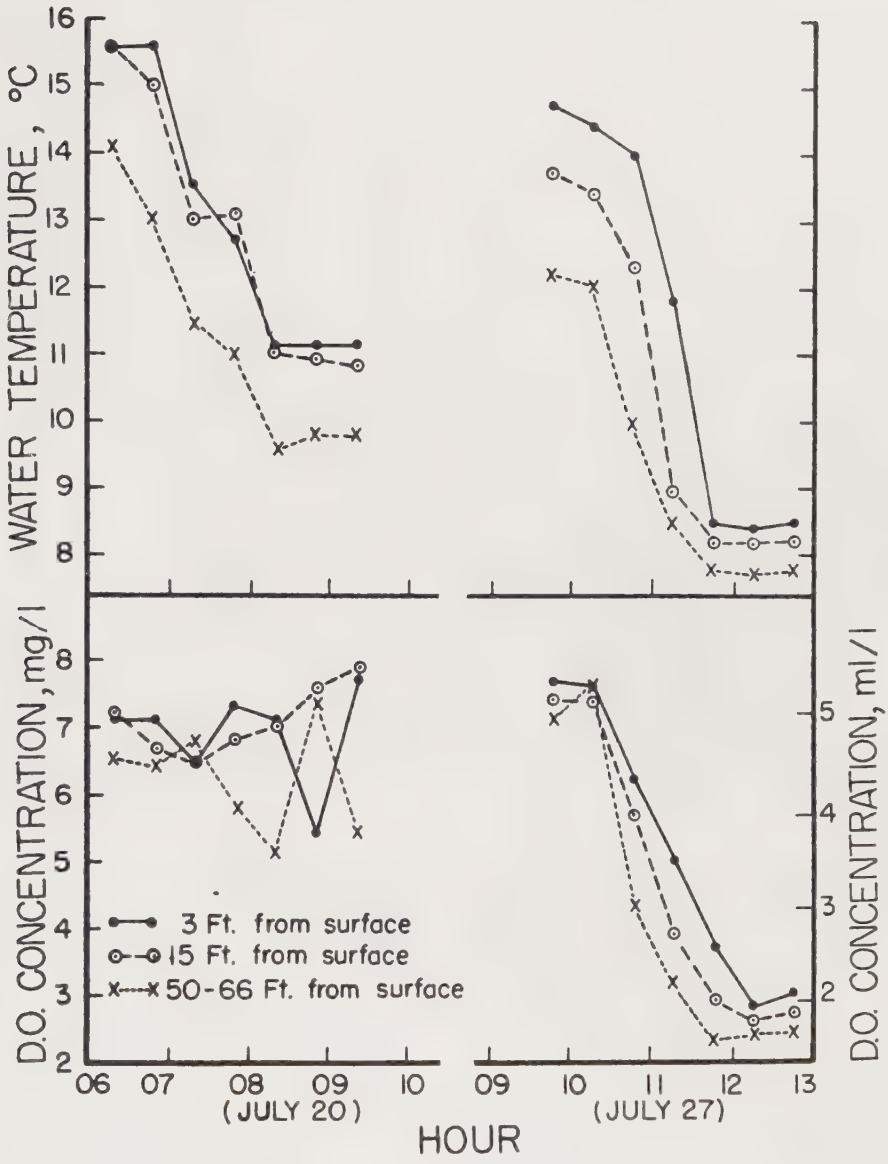


Fig. 4. Temperature-dissolved oxygen concentration relationship for two consecutive sampling surveys, Grays Harbor entrance, 1956.

the temperatures associated with the oxygen deficient water of July 27 were generally at least two degrees colder than those of July 20.

The water temperatures of samples collected on two days during inflow of oxygen deficient ocean water at Grays Harbor entrance are plotted with respect to time after low tide in Figure 5. The dissolved oxygen concentrations are also shown for convenience. The high correlation between water temperatures and dissolved oxygen concentrations for all samples on July 27, 1956, and for the bottom samples of August 30, 1957, is readily apparent. The lack of correlation of water temperature and dissolved oxygen content of the 3- and 15-ft samples of August 30 undoubtedly is due to atmospheric diffusion of oxygen and mixing in the upper layers.

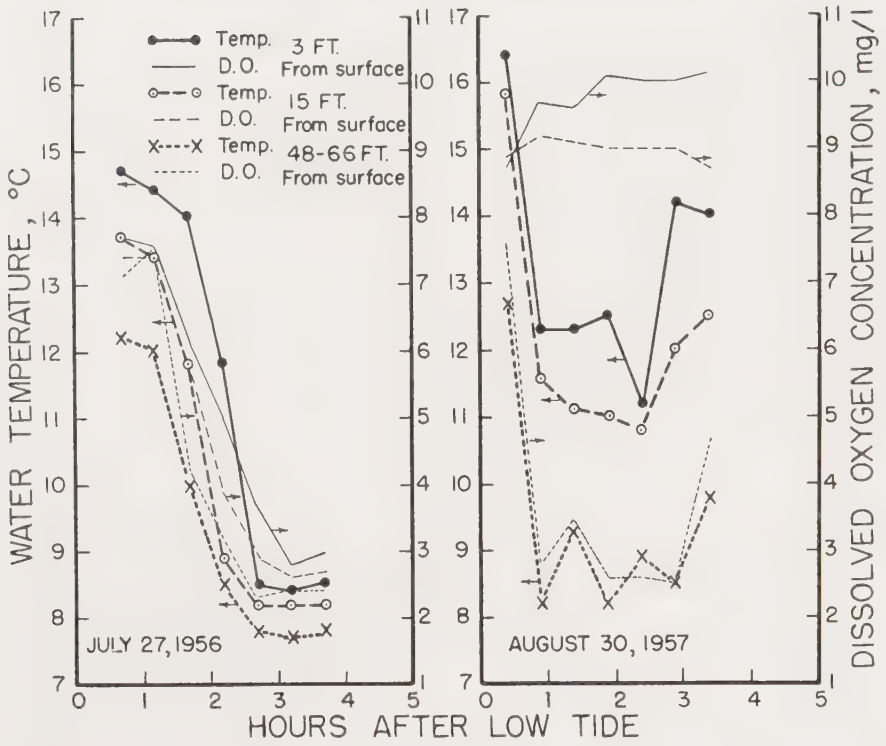


FIG. 5. Temperature and dissolved oxygen characteristics of incoming ocean water, Grays Harbor entrance, Buoy 9.

Oxygen deficient water was observed most frequently during August; however, significant oxygen deficient water was also recorded during the months of July and September. This is in agreement with meteorological considerations of upwelling, as mean surface winds during this period are north-northwesterly due to the northward displacement of the "Pacific anticyclone" in the summer months (Byers 1944) and the mean wind speed is then greater (Mintz and Dean 1952). The reported surface winds for 1956 indicated that the prevailing northwesterlies became of significant velocity and persistence for the occurrence of upwelling during June; and for 1957, during August.

Areal extent of upwelling

A limited number of surveys were conducted to define the extent of upwelling off Grays Harbor entrance. Figure 6 gives the results of one such survey on September 4, 1951, where the upwelled water deficient in dissolved oxygen was observed as far seaward as the survey extended. In fact, approximately three nautical miles offshore near Whistle Buoy 2 the dissolved oxygen levels were as low as 1.5 mg/L (1.0 ml/L) at a depth of 45 ft (approximately 20 ft from bottom).

DISCUSSION

Effects of upwelling on pollutional analyses

The effect of upwelling and low dissolved oxygen levels in the incoming water on the general oxygen level within the harbor is significant. On July 27, 1956, the average dissolved oxygen level of all samples taken at Buoy 9 during the four-hour period monitored was 4.6 mg/L (3.2 ml/L). Assuming that the data reported at Buoy 9, in mid-channel, are representative of the oxygen characteristics across the entire entrance section and that the four-hour period provides a representative sample of the entire

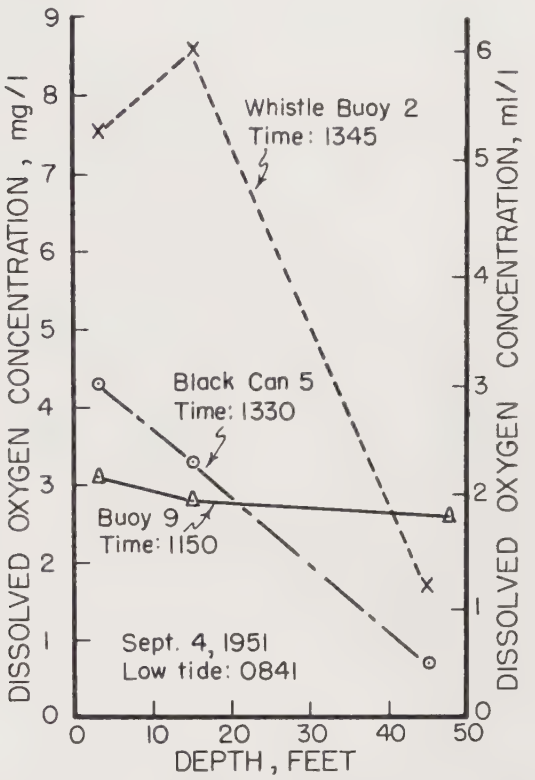


FIG. 6. Typical variation of dissolved oxygen with depth, Grays Harbor entrance, September 4, 1951.

flood water, an estimate can be made of the oxygen deficiency below saturation of the incoming ocean water which fills the harbor tidal prism. In most estuarial oxygen balances the incoming ocean water is assumed to be saturated with dissolved oxygen.

The Grays Harbor tidal prism volume (for a 10 ft tide at the Grays Harbor Port Dock) has been reported by Eriksen and Townsend (1940) to be about 18×10^9 cu ft. Since the tidal range for July 27, 1956, was about 8.5 ft, the actual tidal prism for that day, or the volume of water passing through the harbor entrance during flood tide, is estimated to be approximately 13×10^9 cu ft. During this period the average saturation was only 52%, or about one-half the amount which had been generally assumed available from the ocean for maintaining a favorable environment in the harbor. The computed oxygen "deficit" or amount less than saturation for the tidal cycle monitored was approximately 1,700 tons of oxygen. Expressed in terms of "population equivalent" (based on 5 day biochemical oxygen demand at ⅛ lb. per capita per day), this oxygen deficit from assumed saturation would be approximately equivalent to the effect of discharge of untreated sewage from 20 million persons.

The quantity of water as well as dissolved oxygen entering Grays Harbor each tidal cycle is more than 30 times greater than that supplied by surface runoff during the summer. For example, during low-river flow periods, the total surface runoff to Grays Harbor may be as low as 1,000 cfs or approximately 43×10^6 cu ft per tidal cycle. Compare this value to $1{,}300 \times 10^6$ cu ft of "new" water from the ocean per tidal cycle if only 10% of the total volume of water entering the harbor is considered to be "new" water. Similar ratios would hold for oxygen supply to the harbor. However, it must be pointed out that in terms of water quality conditions in the upper harbor near the major sources of waste discharge, a given volume of fresh water inflow at the head of

the estuary is far more effective in flushing the harbor than the same volume entering from the ocean.

Based on the rather consistent relationship between unusually low water temperatures and low dissolved oxygen concentrations of the incoming ocean water at Grays Harbor entrance, it appears that these conditions are the result of upwelled deep ocean water on the coastal shelf. On a typical day when apparent upwelled water occurred at the harbor entrance, it was estimated that the dissolved oxygen deficit from saturation of ocean water entering Grays Harbor during a tidal cycle was 1,700 tons. Consequently it appears that upwelling phenomena may negate conclusions based on oxygen balances employed in pollutional analyses of estuaries unless the actual dissolved oxygen concentrations at the ocean source are evaluated.

REFERENCES

Byers, H. R. 1944. General Meteorology. New York, McGraw-Hill Company, Inc., 645 pp.

Eriksen, Anne, and L. D. Townsend. 1940. The occurrence and cause of pollution in Grays Harbor. Washington State Pollution Series No. 2, 100 pp.

Hadaka, Koji. 1954. A contribution to the theory of upwelling and coastal currents. Trans. A. G. U., **35**: 431–444

Mintz, Y. and G. Dean. 1952. The observed mean field of motion of the atmosphere. Geophysical Research Papers, **17**: 65 pp.

Saito, Yasukozu. 1956. The theory of the transient state concerning upwelling and coastal currents. Trans. A. G. U., **37**: 38–42.

Stevenson, R. E., and D. S. Gorsline. 1956. A shoreward movement of cool subsurface water. Trans. A. G. U., **37**: 553–557.

Sverdrup, H. U. 1938. On the process of upwelling. Jour. Mar. Res., **1**: 155–163.

Sverdrup, H. U., M. W. Johnson, and R. H. Fleming. 1956. The Oceans. New York, Prentice Hall, Inc., 1087 pp.

ENUMERATION OF FRESHWATER PHYTOPLANKTON CONCENTRATED ON THE MEMBRANE FILTER[1]

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ABSTRACT

Individuals of the phytoplankton become distributed at random when concentrated on the membrane filter. The percentage of microscopic fields in which a species occurs may therefore be validly converted to a theoretical average number of individuals per field. The theoretical density thus obtained and the actual density determined by time-consuming counting are very nearly similar values when 25 or more fields are scored. An enumeration technique using this relationship is described. It has many advantages over commonly used procedures for concentrating the plankton and estimating the number of individuals in a sample.

INTRODUCTION

The membrane or molecular filter that was developed in the United States was first described by Goetz and Tsuneishi (1951). They perfected this filter as a device for concentrating and *in situ* culturing of bacteria. A number of papers (Jannasch 1953, 1958, Ehrlich 1955, Ecker and Lockhart 1959) have recently appeared describing techniques for counting stained bacteria on filters rendered transparent with cedar oil. In these studies, the total number of organisms in a sample was determined by making counts of a representative number of microscopic fields. Goldberg *et al.* (1955) advise the use of similar methods to study marine plankton.

In comparison to the standard plankton concentrating and enumerating devices, the membrane filter offers a number of inherent advantages heretofore unexploited. It is the purpose of this paper to describe and substantiate statistically a rapid technique for the enumeration of freshwater phytoplankton.

[1] The substance of this paper was contained in an address before the Midwest Benthological Society, 6th annual meeting, Madison, Wisconsin, April 17, 1958. Appreciation is expressed to Dr. A. D. Hasler, Zoology Department, University of Wisconsin for his perusal of the manuscript and for making valuable suggestions for its improvement.

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THE PROCEDURE

The organisms are fixed by the addition of four parts of 40% aqueous solution of formaldehyde to each 100 parts of sample. The material is thoroughly agitated and an aliquot is withdrawn using a large-bore pipette. The size of the aliquot is such that an optimum quantity of suspended matter is deposited on the filter. If too large an aliquot is filtered, the organisms will accumulate on top of each other or will be so closely crowded as to make visual separation difficult. Conversely, if the amount is too small, the organisms are spaced at such a distance as to make the enumeration process unduly tedious. With experience, the investigator is able to determine the optimum amount of sample by the appearance of the water.

The aliquot is placed in the tube of a filter apparatus designed to accommodate a one-inch diameter membrane.[3] The water is drawn through the filter by a vacuum-pump. The filter is removed from the apparatus and placed on a glass slide. Two or three drops of immersion oil are placed over the residue and the slide is stored in the dark to dry. The oil replaces the water in the interstices of the filter in approximately 24 hours at room temperature and makes the filter transparent. If protected from light and warm temperature, it has been

[3] Type HA Millipore membrane filters, a product of the Millipore Filter Corporation, Bedford, Massachusetts, were used in this study.

found that the algae cells will retain their coloration and shape for a period in excess of 22 months.

When the investigator is ready to count, a coverslip is placed over the transparent filter and the slide is placed in position on the mechanical stage of the microscope. At this point it is necessary to choose the magnification best suited for scoring the particular sample. In certain instances, low-power is sufficient to recognize clearly all of the forms present. In other cases, it may be advisable to use high-dry magnification or an oil immersion objective lens to identify minute forms. A combination of two or more magnifications can of course be used with suitable conversion factors.

The most abundant species is determined by scanning the filter. A sampling field or quadrat is chosen of such a size that it will contain individuals of this species approximately 80% of the time. The slide is moved about in a random manner so that several such quadrats are observed and the number of them in which the most common species occurs is recorded. If it appears that the percentage of occurrence is substantially lower than 80%, the procedure should be repeated using a larger quadrat; if above 90%, a smaller quadrat should be used.[4] The quadrat size is easily manipulated by using portions of a Whipple micrometer that has been inserted into the ocular of the microscope.

Having proceeded thus, enumeration is begun. The mechanical stage is moved about so that 30 random quadrats are viewed. The presence or absence of individuals of each species encountered is recorded. It is not necessary to count the number of individuals of each species, but only to record whether a certain species is present or absent in each field. When the scoring of 30 quadrats is complete, the frequency-percentage, (F), is calculated for each species by use of the following formula:

$$F = \frac{\text{total number of occurrences of a species}}{\text{total number of quadrats examined}} \times 100$$

Assuming random distribution of individuals on the filter, frequency-percentages may be converted to a theoretical average number of individuals per quadrat. This value is referred to as the theoretical density and is designated by (d). Conversion factors taken from Fracker and Brischle (1944) are given as Table 1. To cite an example, if species A were to have a frequency-percentage of 33.3, its (d) value would be 0.40. Having estimated values for (d), the number of each species per liter can be computed from the following formula:

$$\frac{(d) \times (\text{area of filter})}{(\text{area of quadrat used}) \times (\text{number liters filtered} + \text{liters formalin added})}$$

These data may be converted to areal or volumetric units. To accomplish this, an estimate of the mean dimensions of each enumerated species is obtained from random measurements of individuals taken from the concentrate of a preserved subsample. Welch (1948) advises the use of an areal standard unit and a volumetric

TABLE 1. *Conversion of frequency-percentage (F%) in 30 quadrats to theoretical density (d) taken from Fracker and Brischle (1944)*

F%	d	F%	d
3.3	0.03	53.3	0.76
6.7	0.07	56.7	0.83
10.0	0.10	60.0	0.91
13.3	0.14	63.3	1.00
16.7	0.18	66.7	1.10
20.0	0.22	70.0	1.20
23.3	0.26	73.3	1.32
26.7	0.31	76.7	1.46
30.0	0.35	80.0	1.61
33.3	0.40	83.3	1.79
36.7	0.45	86.7	2.02
40.0	0.51	90.0	2.30
43.3	0.57	93.3	2.71
46.7	0.63	96.7	3.42
50.0	0.69	100.0	?

[4] A value of 80% is selected as optimum since the approximate straight-line relationship that exists between F% and d (see Table 1) from zero to 80% does not hold beyond that point. Also with the most common species occurring in approximately 80% of the quadrats, a larger number of rare species will be encountered than if some lower percentage were selected for the most common form.

standard unit defined as having 400 square microns and 8000 cubic microns respectively.

BASIS FOR THE ACCEPTANCE OF THE TECHNIQUE

The validity of the conversion of frequency values, (F), to theoretical density, (d), is based on the assumption that the organisms are randomly distributed on the filter. A number of indices are available to test this hypothesis, one of the more readily calculated being that developed by McGinnis (1934):

$$K = D/d$$

where K is the deviation from randomness and D is the actual density or the average number of organisms per field as determined by counting. A value of one for K indicates randomness. Values in the neighborhood of 0.5 or lower indicate that the individuals encountered are more scattered than would be expected by chance alone. Values near 2.0 indicate that the individuals are more aggregated than would be expected by chance.

The K value was determined for each species that was encountered in samples taken from three different water sources by both counting individuals and scoring frequency. The quantity of suspended matter varied widely. The most abundant phytoplankton organisms in some samples were colonial forms such as *Anabaena circinalis, Aphanizomenon flos-aquae,* and *Microcystis aeruginosa,* while in others, small unicellular species of *Chamydomonas, Oocystis,* and *Chlorella* were dominant. The size of the aliquot, the magnification, and the area of the quadrat used to score the samples varied. As will be seen in Table 2, the organisms were found to be distributed at random, with K values of all species being close to one.

Loeffler (1954) applied a technique whereby it is possible, if the organisms are distributed at random, to determine the number of quadrats that need be observed in order to obtain a reliable theoretical density value. While compiling data to demonstrate random distribution, the number of individuals of each species occurring in everyone of 40 fields was recorded. Estimates of actual and theoretical density, and so values for D/d, were obtained at each field interval. Only after 25 quadrats were recorded did K tend to stabilize at a value near unity. Consequently, 30 fields were chosen as an adequate number to score.

TABLE 2. *Random Distribution of Phytoplankton on the Membrane Filter*

Organism	F%	D	d	K
Actinastrum sp.	13.3	0.13	0.14	0.9
Anabaena circinalis	40.0	0.50	0.51	1.0
Ankistrodesmus spp.	23.3	0.27	0.26	1.0
Aphanizomenon flos-aquae	90.0	2.80	2.30	1.2
Aphanocapsa sp.	13.3	0.13	0.14	0.9
Asterionella sp.	26.7	0.30	0.31	1.0
Chlamydomonas spp.	73.3	1.47	1.32	1.1
Chlorella ellipsoidea	90.0	2.03	2.30	0.9
Chlorella vulgaris	16.7	0.17	0.18	0.9
Cyclotella sp.	36.7	0.40	0.45	0.9
Euglena spp.	16.7	0.20	0.18	1.1
Fragilaria spp.	16.7	0.17	0.18	0.9
Melosira sp.	66.7	1.30	1.10	1.2
Micractinium pusillum	86.7	2.17	2.02	1.1
Microcystis aeruginosa	30.0	0.33	0.35	0.9
Navicula spp.	13.3	0.13	0.14	0.9
Nitzschia sp.	10.0	0.13	0.10	1.3
Oocystis sp.	63.3	1.07	1.00	1.1
Phacotus sp.	50.0	0.67	0.69	1.0
Scenedesmus spp.	20.0	0.20	0.22	0.9
Selenastrum minutum	36.7	0.47	0.45	1.0
Synedra sp.	26.7	0.27	0.31	0.9
Trachelomonas spp.	73.3	1.40	1.32	1.1

An analysis of variance (Steel and Torrie, unpublished) was done on a set of data compiled by drawing five aliquots of equal size from the same water sample, concentrating the plankton from these on five filters, and enumerating each filter four times. The result of each enumeration was expressed as the summation of the theoretical densities of the individual species. The large phytoplankton organisms were scored at a magnification of 150× and the minute forms at 1455×. The results appear in Tables 3 and 4 and show that the differ-

TABLE 3. *Analysis of variance of individual enumerations of macrophytoplankton concentrated on membrane filters*

Source of Variance	df	SS	MS	F
Among Filters	4	0.898	0.225	<1.00 (ns.)
Within Filters	15	5.685	0.379	
Total	19	6.583		

TABLE 4. *Analysis of Variance of Individual Enumerations of Microphytoplankton Concentrated on Membrane Filters*

Source of Variance	df	SS	MS	F
Among Filters	4	0.114	0.028	<1.00 (ns.)
Within Filters	15	1.803	0.120	
Total	19	1.917		

ences among individual enumerations were not significant.

The coefficient of variation for the enumerations of the macrophytoplankton was:

$$\frac{\sqrt{0.379}}{3.693} \times 100 = 16.7\%$$

The micro-organism enumerations resulted in a similar value:

$$\frac{\sqrt{0.120}}{1.977} \times 100 = 17.5\%$$

APPRAISAL OF THE TECHNIQUE

The advantages of the technique are considerable. The membrane filter retains even the smallest organisms in such a manner that they are randomly distributed in virtually a single plane on the surface of the filter. It has been observed by various workers (Prescott 1951, Moore 1952, Kutkuhn 1958) that counts made in a small number of fields using the Sedgewick-Rafter cell or preparations of concentrated drops are apt to yield inconsistant results due to the non-random distribution of the organisms in the mounts. Most mounts of this type, because of their structural design, prohibit the use of high-dry and oil immersion magnification in enumerating the nannoplankton. Palmer and Maloney (1954) have indicated that such is the case for Sedgewick-Rafter cells. They present data to show that the nannoplankton is likely to be grossly underestimated when enumerated at magnifications inadequate for visual recognition of the material. Lund *et al.* (1958) have found that the nannoplankton concentrated in Utermöhl cells cannot be accurately enumerated with the inverted microscope. If necessary, an oil immersion objective lens may be conveniently used to score the nannoplankton on the membrane filter.

The time consumed in handling a single sample is relatively short, assuming familiarity with the plankton and the procedure. Staining the organisms is not necessary. It takes a few seconds to concentrate the material and 24 hours for the filter to become transparent at room temperature. Oil covered mounts may be stored for an extended period without damage to the cells. Approximately 10 minutes are required for the enumeration. The time consuming process of counting individual cells is eliminated.

The filter apparatus is compact and light in weight. It may be operated in the field by employing a small handpump to develop the necessary vacuum. Oil covered filters rather than bulky quantities of water may be returned to the laboratory for analysis.

The major disadvantages of the technique are inherent in many other methods as well. Live forms are not observed. Delicate cell or colonial envelopes, flagella, and the like are not easily visible. Movements cannot be observed. These difficulties can be overcome by subdividing the sample prior to fixation and studying the live material.

The described procedure may be variously modified to meet the needs of a specific investigation. Unfixed material may be concentrated on the filter with some distortion. If time is important, the filter may be dried by drawing air through it for one minute and immediately be rendered transparent with cedar oil. The technique as presented above provides for the enumeration of only the most common organisms. Clearly, if one wants to minimize the number of species which will be missed altogether, the number of quadrats scored may be increased beyond 30.

REFERENCES

ECKER, R. E., AND W. R. LOCKHART. 1959. A rapid membrane filter method for direct counts of microorganisms from small samples. J. Bacteriol., **77**: 173–176.

EHRLICH, R. 1955. Technique for microscopic count of microorganisms directly on membrane filters. J. Bacteriol., **70**: 256–268.

FRACKER, S. B., AND H. A. BRISCHLE. 1944. Measuring local distribution of *Ribes*. Ecol., **25**: 285.

GOETZ, A., AND N. TSUNEISHI. 1951. Application of molecular filter membranes to the bacterial analysis of water. J. Amer. Wat. Wks. Assoc., **43**: 943–984.

GOLDBERG, E. D., M. BAKER, AND D. L. FOX. 1955. Microfiltration in oceanographic research. I. Marine sampling with the molecular filter. J. Mar. Res., **11**: 194–204.

JANNASCH, H. W. 1953. Zur Methodik der quantitativen Untersuchung von Bacterien-Kulturen in flüssigen Medien. Arch. Mikrobiol., **18**: 425–430.

JANNASCH, H. W. 1958. Studies on planktonic bacteria by means of a direct membrane filter method. J. Gen. Microbiol., **18**: 609–620.

KUTKUHN, J. H. 1958. Notes on the precision of numerical and volumetric plankton estimates from small-sample concentrates. Limnol. Oceanogr., **3**: 69–83.

LOEFFLER, R. J. 1954. A new method of evaluating the distribution of planktonic algae in freshwater lakes. Ph.D. Thesis, Univ. of Wis. Library, Madison, Wis.

LUND, J. W. G., C. KIPLING, AND E. D. LECREN. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia, **9**: 143–170.

MCGINNIS, W. G. 1934. The relation between frequency index and abundance as applied to plant populations in a semi-arid region. Ecol., **15**: 263–282.

MOORE, E. W. 1952. The precision of microscopic counts of plankton in water. J. Amer. Wat. Wks. Assoc., **44**: 208–216.

PALMER, C. M., AND T. E. MALONEY. 1954. A new counting slide for nannoplankton. Am. Soc. Limnol. Oceanogr. Special Publ. No. 21, 6 pp.

PRESCOTT, G. W. 1951. The ecology of the Panama Canal algae. Trans. Am. Micro. Soc., **70**: 1–24.

STEEL, R. G. D., AND J. H. TORRIE. Principles and procedures of statistics with special reference to the biological sciences. Unpublished manuscript, Agronomy Dept., Univ. of Wis., Madison.

WELCH, P. S. 1948. Limnological methods. Blakiston Co., Philadelphia, Pa.: 290–295.

COMPARATIVE LABORATORY AND FIELD STUDIES OF PHOTOSYNTHESIS BY A MARINE PLANKTONIC DIATOM[1]

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ABSTRACT

A study is described of the factors affecting measurements of phytoplankton photosynthesis by the much used field method, based upon changes of oxygen concentration in clear and darkened bottles as determined by the Winkler method. Unialgal cultures of a marine plankton diatom, *Chaetoceras affinis*, were used with short exposures of 1–3 hours in both laboratory and sea. Indications of a limitation of photosynthetic rate by inadequate CO_2 supply were only found for culture media with pH raised by prolonged photosynthesis. Otherwise photosynthetic rates were unaltered by the bicarbonate concentration over a wide range, including that of unenriched sea-water, or by cell sedimentation in unshaken cultures. A comparison of the Winkler and manometric methods of measuring oxygen production gave very similar results. High rates of photosynthesis were well maintained over the main period of each exposure, despite the development of oxygen supersaturation. Lower rates were however always found during an initial induction phase.

Photosynthetic characteristics deduced from exposures in laboratory and sea, carried out almost simultaneously and with the same algal material, were in general agreement. Data from the experiments as a whole indicated the development of unusually high photosynthetic capacities at light saturation, assessed per unit content of chlorophyll *a*. The onset of light saturation, and the development of photo-inhibition, occurred at intensities similar to those recorded for many other plankton algae. Some ecological implications of the findings are discussed.

INTRODUCTION

Knowledge of the photosynthetic activities of natural populations of planktonic algae has been obtained from experiments in both laboratory and field. Each of these approaches has limitations. The laboratory experiment may provide well-defined data on the photosynthetic characteristics of the organisms, but any deduction of the distribution of photosynthetic activity in the natural environment of sea or freshwater involves uncertain extrapolations, even when given a better knowledge of environmental variables than is usually available. The field experiment, with exposures made in the water-body itself, may appear to give more directly applicable results, and indeed has been the source of most information on the subject. Nevertheless, although the data obtained may be valid for the local conditions of the experiment, they are usually unsuitable for a quantitative analysis of the principal factors involved, and so are difficult to incorporate into a generalized body of knowledge on the photosynthetic behavior of planktonic algae. The obstacles here arise partly from the heterogeneous nature of the populations sampled, and partly from difficulties of measuring the relevant environmental factors, such as light intensity, which may fluctuate considerably during an experiment.

Comparative laboratory and field experiments, using the same well-defined algal material, provide a means of integrating the two approaches. This paper describes such studies. Photosynthesis was followed by measuring the oxygen produced by *Chaetoceras affinis* Lauder during exposures in bottles suspended at various depths in the Pacific Ocean, and was compared with results from almost simultaneous exposures under a range of light intensities in the laboratory. Particular study was made of the relation between photosynthetic rate and light intensity in these two situations. Possible limitations in the method of determining photosynthesis by exposures of algal suspensions in closed bottles were explored,

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and several photosynthetic characteristics of the diatom used were determined. The results are relevant to similar work in which photosynthetic activity is measured from the uptake of radioactive carbon (C^{14}).

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MATERIALS AND METHODS

Unialgal cultures of *Chaetoceras affinis* were used throughout. This species had been isolated by Dr. B. M. Sweeney from Pacific coastal water and maintained in culture at the Scripps Institution of Oceanography for several years. It was chosen because of its ease of culture and fast growth of up to at least two cell divisions per day at 15°C. The species is widely distributed in coastal and offshore waters of the Pacific and other oceans. Although pronounced morphological aberrations were not found in healthy cultures, auxospore formation occasionally developed, with corresponding changes in average cell size, during the course of these experiments. Cultures were grown, and most of the following measurements of photosynthesis made, in an enriched sea-water medium containing 75% filtered sea-water. Its composition was based upon that used for *Gonyaulax polyedra* by Sweeney and Hastings (1957), modified by the addition of 5 mg/L of silicon (added as $Na_2SiO_3 \cdot 9\ H_2O$) and of various concentrations of potassium bicarbonate as described later. The large cultures intended for measurements of photosynthesis were grown in 2.5 L flasks at 14–16°C in a constant temperature room. An illumination of approximately 5,400 lux was provided by two fluorescent lamps below the cultures. Cultures were used when they had reached densities of 19,000–46,000 cells per ml, which were still considerably lower than the maxima attainable, about 100,000 cells per ml.

Photosynthesis was followed from changes in the concentration of dissolved oxygen, determined by the Winkler method. Samples of 100 ml were titrated with approximately N/160 thiosulphate, standardized with N/10 potassium dichromate solution. Exposures were made with the algal suspension distributed in ground-glass stoppered bottles of 'Pyrex' glass, capacity about 120 ml, filled from a siphon in a darkened room. Both clear and dark bottles were used in each exposure, and the gross photosynthesis, corrected for respiration, was obtained from the difference between them. Laboratory measurements were carried out with the bottles supported horizontally in a constant temperature water-bath, and illuminated from a bank of five 'daylight' fluorescent lamps placed immediately below the glass base of the bath. Minimum spacing between fluorescent tubes in the bank and between the bank and the bottles gave maximal illumination in the bottles of 2,100–2,500 lux. Each lamp was used with two ballasts connected in parallel to increase its total output. Three lower light intensities could also be obtained in a sequence along the long axis of the water-bath, using neutral filters made from exposed photographic film mounted in glass and placed on the bottom of the bath. The neutral transmission of the filters, in the spectral region 400–700 mμ, was checked spectrophotometrically. Three bottles could be inserted above each neutral filter, in a compartment isolated optically from its neighbors by partitions of blackened plastic. Owing to the extended nature of the light source, differences of light intensity across the depth of each bottle were negligible. Intensities at the levels of the bottles, on a plane perpendicular to the direction of the light source, were measured with a selenium rectifier-cell photometer (Weston model 756) calibrated in foot-candles but here converted to meter-candles or lux. The energy content of the radiation was also measured with a thermo-

pile, yielding an interrelation of 44 ergs/cm²/sec per foot-candle recorded by the photo-cell or 4.1 ergs/cm²/sec per lux.

Field exposures were made near a fixed buoy in the ocean about one km. from the shore and laboratory. Bottles were filled with algal suspension in the darkened laboratory and transported in a dark container to this station. Here they were attached by spring clips to metal rings of approximately 60 cm diameter, and the latter fastened to a rope which supported both rings and bottles horizontally at various depths in the sea. The arrangement was devised as a modification of that described by Levring (1947), and enabled up to 9 bottles to be supported horizontally at any desired depth. Dark bottles exposed at several depths yielded almost identical values for respiratory oxygen uptake, which as in dark bottles in laboratory experiments was only a small fraction (0.05–0.2) of the maximum photosynthetic rate. As the sea exposures described here were of short duration, of one to one and a half hours, and were carried out in full sunshine about midday or early afternoon, changes in the intensity of incident solar radiation were small, not exceeding ± 10%. Continuous records were taken with an Eppley thermopile ('pyrheliometer') situated on the roof of the laboratory and used to calculate the mean irradiation on a horizontal surface during each experiment. Radiant energy in the spectral region available for photosynthesis was taken as 0.46 of the total energy recorded (Talling 1957a).

Light intensities at various depths in the ocean were calculated from the surface intensity, reduced by 5% representing surface loss (estimated from the solar elevation and data in Davis 1941 and in Anderson 1952), and measurements of underwater light penetration. The latter were made with a selenium rectifier photo-cell (Weston model 856 RR) in conjunction with red, green and blue Corning glass filters. Measurements were restricted to the linear region of the current-intensity characteristic of the photocell, corresponding to photo-currents below 700 μa. The mean extinction midpoints of the cell-filter combinations, in their working depth ranges, were estimated as respectively 450, 525, and 625 mμ; these values were calculated from the spectral sensitivity of the cell, spectral transmission of the color filters, and color-filter action of the seawater. Values of the percentage transmission (T) per meter were derived from measurements in each spectral region. They were compared with the families of curves obtained by Jerlov (1951, Fig. 48) to describe the variation of T with wavelength in the spectral region 400–700 mμ, from which data for the spectral regions between the experimental points were interpolated. Using the resultant curves for the spectral variation of T, and the data of Taylor and Kerr (1941, Fig. 8, curve D) for the spectral distribution of energy in the surface-incident light, the spectral distribution of energy (400–700 mμ) was calculated for the depths at which photosynthesis was measured. Planimetric integration of the areas under these spectral distribution curves (see, Sverdrup, Johnson and Fleming 1942, p. 105) enabled the total radiant energy (400–700 mμ) at each depth to be expressed as a percentage of the sub-surface intensity. Knowing the latter, the absolute irradiation at each depth could be calculated. The results were very similar to those derived by a more approximate procedure (used by Jenkin 1937 and Talling 1957a) in which the radiant energy is divided between a few spectral blocks whose contributions are summed for each depth. In these field experiments the water-column showed an optical discontinuity, with more turbid water below (Figs. 5 and 6); consequently the calculation outlined above had to be performed in two stages.

Considerable vertical stratification was also shown in the depth-distribution of temperature, which was measured during each experiment with a bathythermograph. Tests were made to determine the rate of equilibration of temperature between the contents of experimental bottles and a colder surrounding medium of flowing water. After 10 minutes exposure the remaining temperature difference was less than 1°C when the initial difference was 7°C; the latter value would not be exceeded under the conditions of the field experiments.

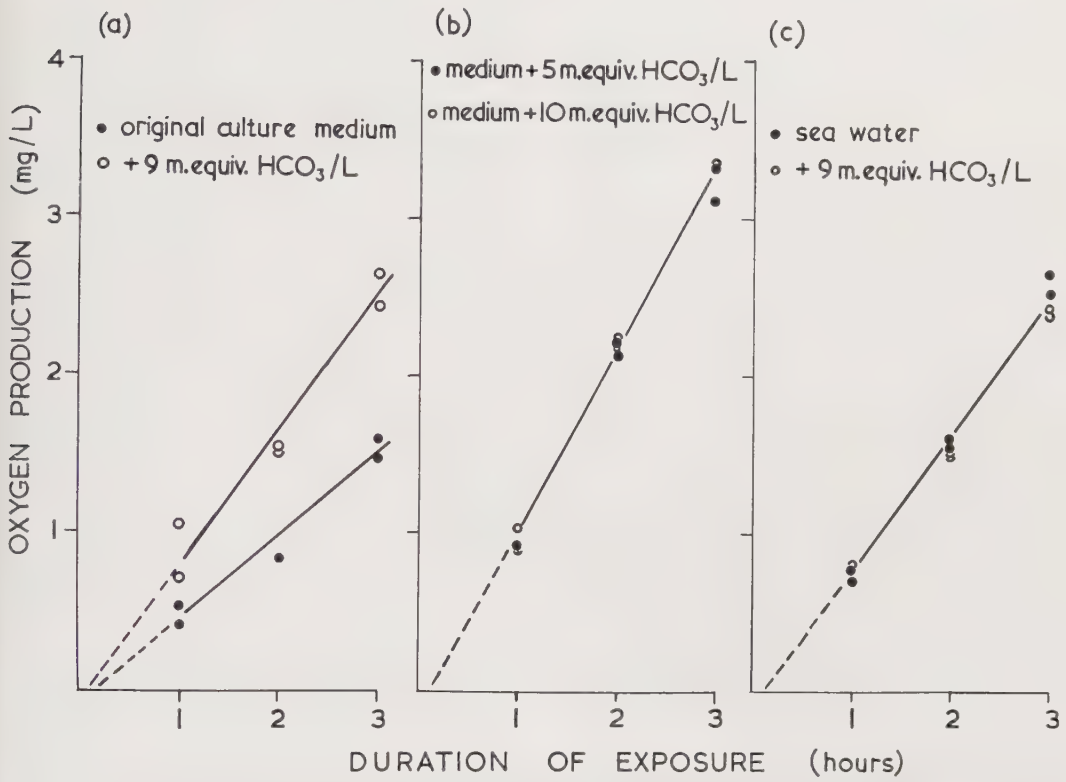

FIG. 1. Photosynthesis in media containing various supplementary additions of bicarbonate. These were made (a) to the original culture medium, (b) to the new culture medium with 5 m equiv of bicarbonate/L, (c) to cells resuspended in filtered sea water.

The densities of the algal suspensions were normally estimated from both cell counts and chlorophyll *a* determinations. Counts were made in duplicate upon volumes of 0.05 ml, counted on a normal microscope slide using the scanning procedure of Utermöhl (1936, Fig. 648). Chlorophyll *a* was estimated by the spectrophotometric method of Richards and Thompson (1952), the cells being first separated by paper filtration. Complete extraction of pigment from the cells was obtained within 3 hours.

FACTORS CONTROLLING PHOTOSYNTHESIS UNDER LABORATORY CONDITIONS

Some knowledge of the factors affecting photosynthesis under laboratory conditions was sought before attempting the analysis of photosynthetic behavior in the sea. Most measurements (in sections i–iii below) were made with high light intensities known to give complete light-saturation of photosynthesis and within a small temperature range (14–16.5°C). The variation of photosynthetic rate with temperature was not determined.

(*i*) *Composition of the medium*—It was clearly desirable to avoid determinations of photosynthesis in unfavorable media, particularly with respect to carbon dioxide and the associated carbonate-bicarbonate buffer system. Figure 1 illustrates comparative measurements of photosynthesis in a number of modifications of the culture medium previously used for the routine subculture of the diatom. The buffer capacity of the original medium was insufficient to prevent a considerable increase of pH (*e.g.* from 8.3 to 9.0) during the growth of cultures to the required density. Photosynthesis in such an alkaline medium (pH 9.0, combined CO_2 1.5–2.0 m equiv/L) is shown in Figure 1a, together with the improved

rate obtained by the further addition of 9 m equiv/L of $KHCO_3$ and concomitant reduction of the initial pH to 8.5. Further experiments (Figs. 1b, 2b) showed that this response to added bicarbonate could be eliminated by the addition of 5 m equiv/L of bicarbonate after autoclaving but before inoculation of the cultures. This new culture medium with increased buffering, in which pH was maintained below 8.7, was adopted in all subsequent work. Nevertheless one experiment (Fig. 1c) showed that cells removed from an original culture by filtration, and resuspended in filtered sea-water of pH 8.3, yielded a rate of photosynthesis equal to that of similar cells resuspended in sea-water, enriched by 9 m equiv/L of bicarbonate at pH 8.1. For short exposures, therefore, in which the demands upon the carbon dioxide supply of the medium are small, sea-water without bicarbonate enrichment would appear an adequate medium. Inadequate buffering appears only after the longer exposures used during growth of the cultures to suitably high densities.

(*ii*) *Agitation of the cell suspensions*—Much criticism (*e.g.*, Emerson and Green 1934, Emerson 1935) has been levelled against measurements of photosynthesis by aquatic plants in unshaken and sealed vessels, particularly when large samples of macrophytes were used. Limitations of gaseous diffusion in unstirred media are likely to be minimal for dilute suspensions of unicellular algae, but few tests of this point are recorded in the abundant ecological literature (see, however, Talling 1957a, Doty and Oguri 1958). An experiment was therefore made to test whether rates of photosynthesis differed between unshaken suspensions in which cells were allowed to sediment and suspensions in which shaking by hand every 15 minutes maintained cells in free circulation. Continuous shaking by horizontal movements, with glass beads in the bottles, was also tested but found to be mechanically inadequate for these completely filled bottles. The experimental results (Fig. 2a) show almost identical rates of photosynthesis in shaken and unshaken bottles, despite a considerable sedimentation of cells which occurred in the latter during the three-hour exposure. Several test conditions were more severe than those likely to prevail in ecological field experiments, notably the high algal density (41.7×10^6 cells, or 0.081 mg chlorophyll *a*/L) and high photosynthetic rate (2.37 mg oxygen /L hour). The latter was the highest rate in the present experiments, being probably accelerated by the higher temperature chosen for this exposure (19.7 ± 0.4°C, compared with 14–16.5°C in all other laboratory experiments).

Rates of photosynthesis under light saturation were also compared, using unshaken Winkler bottles and continuously shaken Warburg manometers, at 15.0–15.5°C. The manometric measurements were carried out by Dr. K. A. Clendenning as follows. All cells were derived from the same culture, of which a portion was concentrated by paper filtration to yield the higher cell densities required for the manometric measurements. The cells were centrifuged from this concentrate and resuspended in fresh growth medium with additions of bicarbonate, giving total bicarbonate enrichments of 5–25 m equiv/L at pH 8.3. The cell density so obtained was 24 times higher than that employed for the Winkler determinations. Under the conditions of the Winkler and manometric measurements, the light-saturated rate of photosynthesis was not increased by raising the bicarbonate enrichment above 5 m equiv/L. The rates of photosynthesis observed manometrically with 5 m equiv/L bicarbonate, during the first hour after induction, were within the range of the corresponding Winkler measurements shown in Figure 2b. The agreement between the two methods is noteworthy in view of the very different conditions of shaking and cell concentration which were involved. Manometric measurements of photosynthesis have been made on another species of *Chaetoceras* by Sagromsky (1943), who could not show any injurious effects of the shaking involved. A direct experimental comparison of the two methods, similar to that described above, appears to be lacking in previous work, despite the extensive literature on each method.

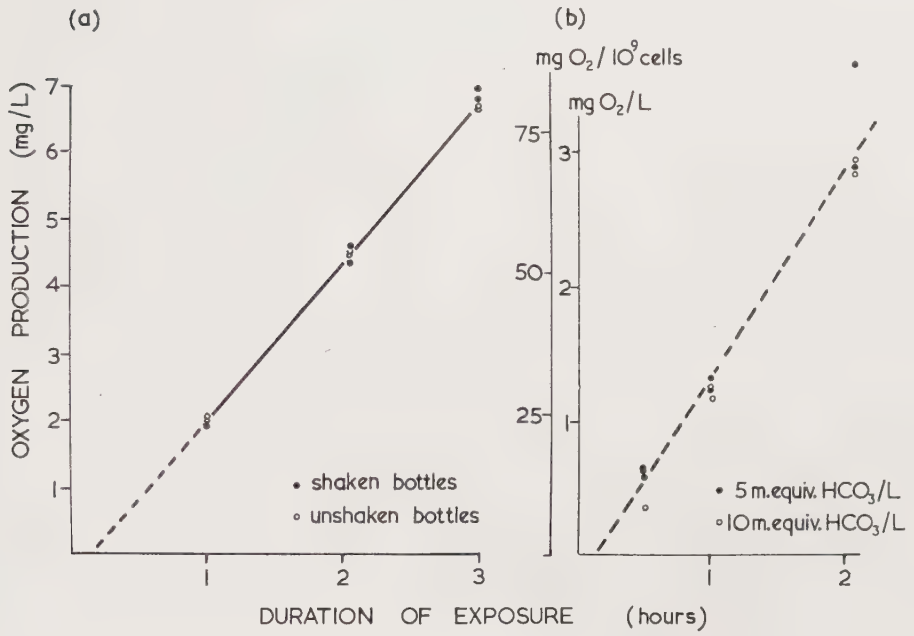

FIG. 2. Photosynthesis in shaken and unshaken cell suspensions, measured by (a) the Winkler method only (b) the Winkler and manometric methods. In (b) the mean rate obtained manometrically is expressed by the gradient of a broken line which is superimposed on Winkler determinations of oxygen production in two unshaken media.

(*iii*) *Variation of photosynthetic activity during exposures*—Measurements of photosynthesis in closed bottles are usually expressed as average rates over the periods of exposure, in which possible short-time changes of activity are not distinguished. Such changes can be followed either by repeated sub-sampling from each bottle, which is impracticable with the Winkler oxygen determination, or by use of replicate bottles which are sampled in succession. Both alternatives are inconvenient in field experiments, but successive sampling of replicate bottles has been used whenever possible in the present laboratory experiments. Results are illustrated in Figures 1, 2 and 3, from which the variation of photosynthetic rate with time can be followed within the exposure limits of 3–3¼ hours used.

In all experiments the time course of photosynthesis shows two general features. An almost constant rate is maintained during the second and third hours of each exposure, despite an increasing supersaturation with oxygen. In the first hour or half-hour the overall rate is lower, and extrapolation shows that it is *equivalent* to a lag of 6–18 minutes succeeded by the rate maintained during most of the exposure. This 'lag-equivalent' is shown by exposures in a wide range of light intensities (Fig. 3), although all these intensities were higher than the very low intensities prevailing when the bottles were being prepared. An induction phase of photosynthesis is therefore likely to occur in all exposures. The 'lag-equivalent' is also seen in exposures involving cells with different photic histories (Fig. 3).

These results clearly imply that rates measured in a single uninterrupted exposure will underestimate the rates finally realized under the same conditions. Thus in the combined laboratory and sea experiments described later with exposures of 1–1½ hours, the probable underestimation is 7–30%. This factor will diminish with increasing length of exposure; its small significance for exposures of 3 hours is illustrated in Figure 3d. Steemann Nielsen and Jensen (1957) have also described lower initial rates of photosynthesis during exposures with a natural

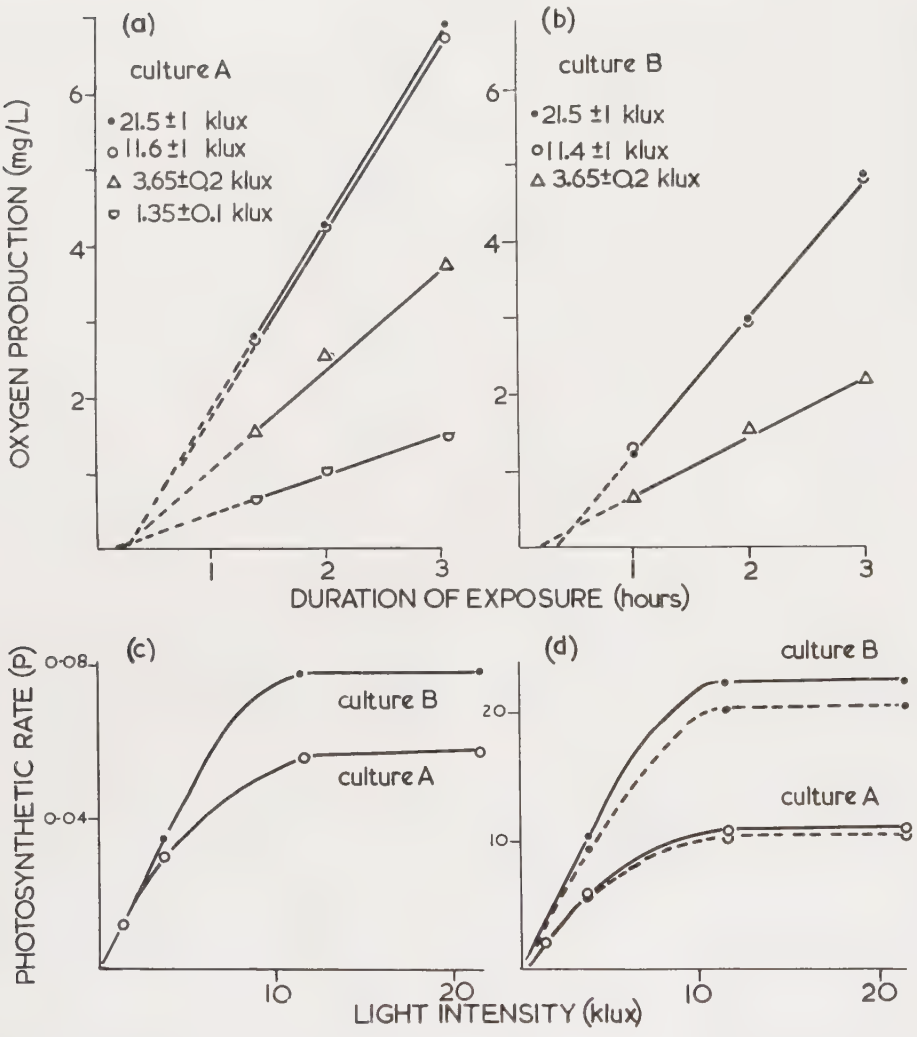

FIG. 3. Photosynthesis–time measurements for two cultures at various light intensities (above), with average gradients inserted and used to derive rate–intensity curves (below). Culture A was grown at 0.97 klux, and B at 5.4 klux, followed by darkness for 2 days. Photosynthetic rates (P) are given in mg oxygen/mm^3 cell volume hour (c) and in mg oxygen/mg chlorophyll *a* hour (d). Broken lines in (d) show the overall rates of photosynthesis during the longest exposures.

population of surface plankton. They attribute this to an after-effect of light-inhibition, an explanation which is not applicable to the present results.

(*iv*) *Light intensity*—Without some knowledge of the relation between photosynthetic rate and light intensity an individual measurement of photosynthesis has little significance, as rates ranging from zero to the light-saturated capacity can be obtained at various intensities. Rates measured at light saturation (here denoted by P_{max}) allow the most direct comparison between laboratory and field experiments. The achievement of such conditions in the laboratory is described below, and the variation of rates with light intensities below saturation is discussed.

The general form of the rate-intensity relation is shown by data from laboratory experiments conducted simultaneously with exposures in the sea (Figs. 5c, 6c). Very similar curves were obtained in four other experiments, not illustrated. An upper

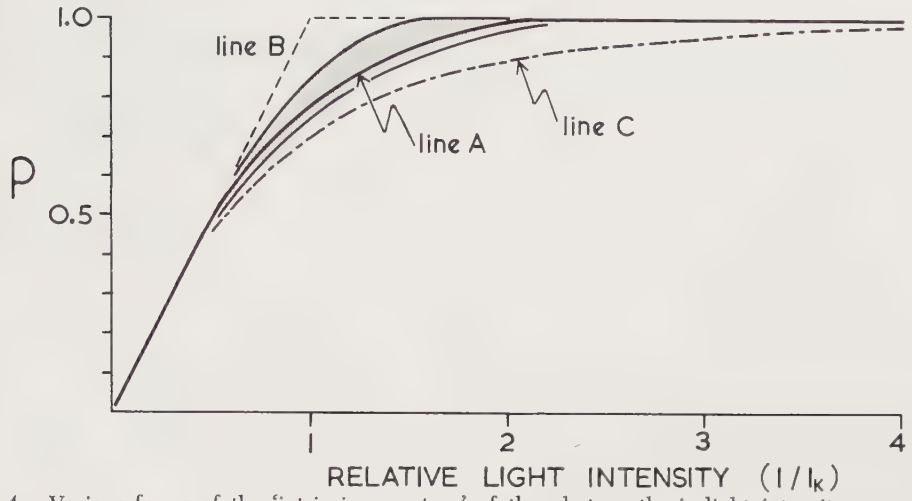

FIG. 4. Various forms of the 'intrinsic curvature' of the photosynthesis–light intensity curves below light saturation. Rates of photosynthesis are expressed as fractions (p) of the rate at light saturation, and light intensities in multiples of the I_K characteristic. The heavy line A indicates the average relation, and the stippled area the range of variation, in the present experiments. Line B shows the initial linear region continued up to the light-saturated rate: line C shows the relationship of Smith (1936, equation 1) here expressed as $p\,(1-p)^{-\frac{1}{2}} = I/I_K$.

'plateau' on the rate-intensity curves provides good evidence that light-saturation is fully realized at the highest intensities used, 24,000–27,000 lux. The onset of saturation in relation to the light intensity scale can be indicated by the intensity at which extrapolations of the initial linear gradient and final saturation 'plateau' intersect (see Fig. 5c; also Kok 1956a, b, Talling 1957a). This intensity, here denoted by I_K, varied little (between 4,600–6,800 lux) in five experiments, all at temperatures between 14 and 16.5°C.

Considerable interest attaches to the form of the 'intrinsic curvature'—the curvature property independent of the absolute scales used—shown by the rate-intensity curves at intermediate light intensities. With P_{max} and I_K variables, it can be used to summarize much of the rate-intensity characteristic. It has received little attention in ecological work, often being completely neglected (*e.g.* by Ryther 1956). Modifications associated with optically dense suspensions (Rabinowitch 1951, p. 1008) are unlikely to be appreciable with the relatively thin suspensions used in this and most other ecological work. The description of such intrinsic curvature is possible either by the application of a mathematical relation (*e.g.* Kok 1956b, Talling 1957a), or by plotting curves with standard scales for the light-saturated rate (P_{max}) and the initial linear gradient. The latter approach is the more flexible and is illustrated in Figure 4. The same figure (line C) shows the form of curvature implied by the relation proposed by Smith (1936, equation 1) and used in several previous studies (*e.g.* Winokur 1948, Talling 1957a). The approach to light-saturation so derived is clearly more gradual than the experimental data indicate. Similar divergence is shown in some, but not all, of the data of Talling (1957a) obtained from studies of a freshwater plankton diatom. Steemann Nielsen and Jensen (1957) have stated that the equation was inapplicable to their rate-intensity curves for marine phytoplankton, but the type of curvature appears variable and the attainment of complete light-saturation is sometimes not established. Other equations, such as that of the rectangular hyperbola, have been tested here with even less success. Consequently the curvature relation is probably best expressed in a standardized graphical form, as in Figure 4, although errors can easily arise in estimating the initial gradient of the curves.

A further experiment was designed to ob-

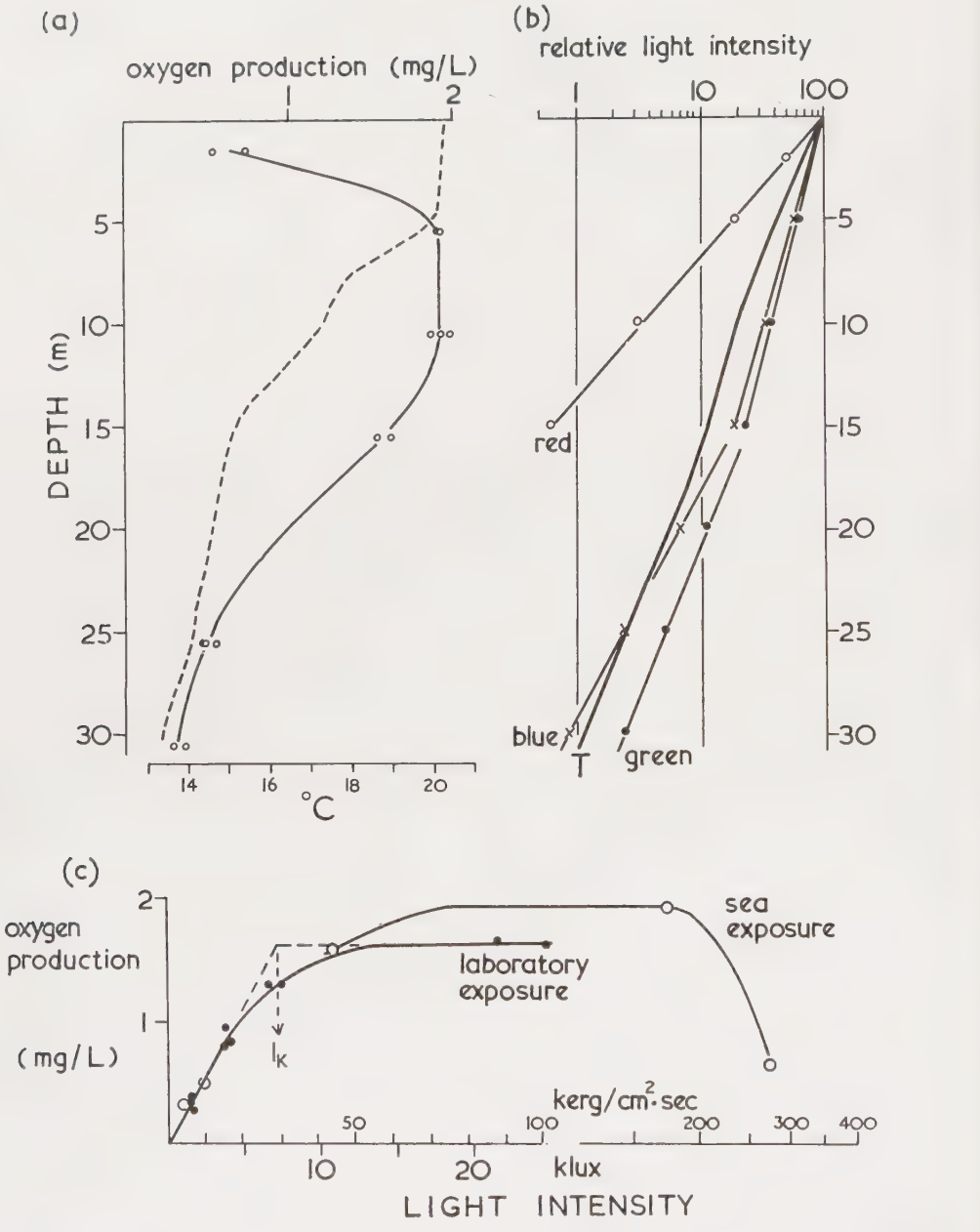

FIG. 5. Combined field and laboratory experiment of 5 Aug., 1957, showing (a) the variation of photosynthetic rate (solid line) and temperature (broken line) with depth, (b) light penetration measured for three spectral regions and of total energy (T) in the region 400–700 mμ, (c) the variation of photosynthetic rate with light intensity (higher intensities shown on a logarithmic scale) obtained from both laboratory and sea exposures.

tain data on the rate-intensity characteristic from exposures in which a time-sequence of determinations enabled the effects of the initially lower rates to be eliminated. The same experiment included a comparison of two sets of cells given different pre-treatments, one being grown at a low intensity of 970 lux, and the other at the normal cul-

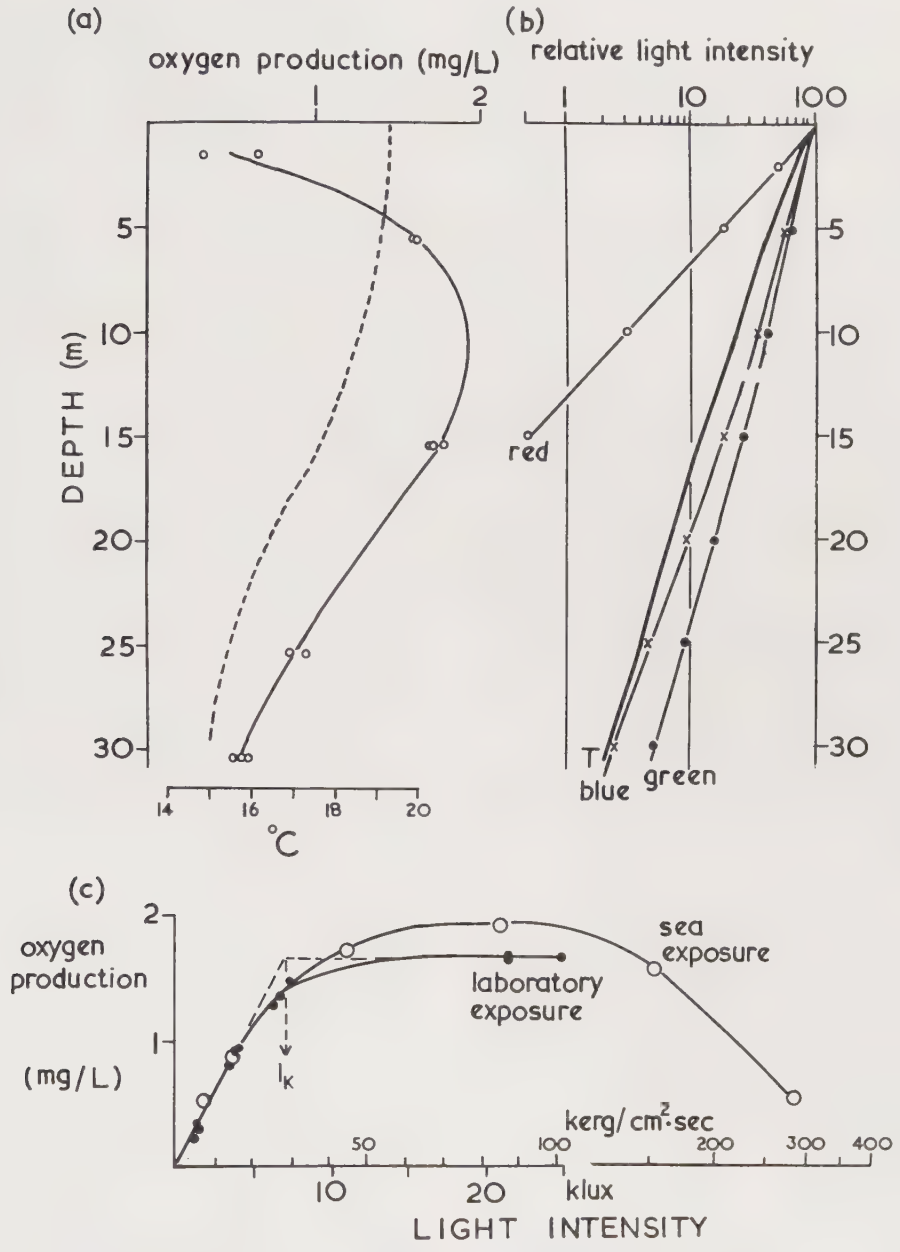

FIG. 6. Combined field and laboratory experiment of 7 Oct., 1957. Representation as in Figure 5.

ture intensity of 5,400 lux but then kept in darkness for two days. Figure 3 illustrates both the original oxygen determinations and the derived rate-intensity characteristics. The latter do not show any appreciable modification in the intensities at which light saturation developed. Similar behavior by cultured populations of several planktonic algae, grown under different types of illumination, is described by Ryther (1956). However, marked modifications have been found in several natural populations, when the characteristics of algae obtained from various depths have been compared (Steemann Nielsen and Hansen 1959, and unpublished experiments of the author).

PHOTOSYNTHESIS IN THE SEA AND LABORATORY COMPARED

Rate-intensity characteristics have been calculated for two experiments, in which simultaneous field and laboratory exposures with the same algal material were made. Figures 5 and 6 illustrate the variation of photosynthetic rate with depth, with the vertical gradient of light intensity expressed for three spectral regions and for the entire visible spectrum (400–700 mμ). From these data the corresponding rate-intensity curves are derived, each depth being replaced by the equivalent light intensity expressed as an energy flux for the 400–700 mμ spectral region. For each experiment direct comparison can be made with the rate-intensity curves obtained in the parallel laboratory exposure with fluorescent illumination. Intensities of the latter are also expressed in terms of energy flux, using the factor noted above; the limits of the spectral region involved (illustrated by Withrow and Withrow 1956, Fig. 3–15) were close to the limits of 400 and 700 mμ adopted in calculating light intensities in the sea. The rate-intensity curves obtained from the sea exposures suffer from various complicating influences connected with the vector distribution and spectral modification of underwater light (see below), so that their correlation with laboratory data is, *a priori*, uncertain. An important difficulty was the presence of vertical gradients of temperature in the sea (see Figs. 5 and 6). The laboratory temperatures, 14.9–16.4°C, were chosen to lie near the centers of the ranges occurring in the photic zone of the sea. Experiments in which the sea surface temperature exceeded 20.5°C are not illustrated.

The variation of photosynthetic rate with depth is of a form familiar from many other studies, both in the sea and freshwater. Much of it can be deduced from the rate-intensity characteristic measured in the laboratory, considered in relation to the almost exponential decrease of photosynthetically active radiation with depth in the sea. The initial linear region of the rate-intensity characteristic corresponds to the lower 'hollow' part of the rate-depth curve; the succeeding 'plateau' region at light-saturation is also reflected, in an abbreviated form, in the depth curve. A partial inhibition of photosynthesis is present at the higher light intensities near the sea surface, which were not attainable with the fluorescent lighting used in the laboratory exposures. The general form of the inhibition, and the intensities under which it developed, resemble those recorded in several other field studies with planktonic diatoms (Jenkin 1937, Talling 1957a). Nevertheless the extent of the inhibition may well depend on the spectral composition of the underwater radiation, particularly in the blue (Kok 1957a) and ultra-violet regions. Consequently the general validity of a calculation of the depth-distribution of photo-inhibition in nature, based on measurements in sunlight reduced by 'neutral' filters (Ryther 1956, Steemann Nielsen 1958, p. 45), is not established. Even direct field measurements of the inhibition may be influenced by the absorption of ultra-violet radiation in the glass walls of the experimental vessels (Gessner and Diehl 1951, Gessner 1955, p. 415). This factor requires further investigation.

Quantitative comparison of the photosynthetic behavior in laboratory and sea exposures can be based upon (i) the rates obtained at light saturation (P_{max}) or (ii) the initial gradients of the rate-intensity curves ($= P_{max}/I_K$). These features have contrasted responses to two factors (Rabinowitch 1951, 1956), temperature and spectral composition of the illumination, which differ between exposures in laboratory and sea. Temperature differences are likely to alter (i) but not (ii), but for spectral differences this situation is reversed. Both characteristics are displayed in Figures 5 and 6, which show considerable agreement between photosynthetic behavior in laboratory and sea. Rates at light-saturation are slightly higher in the sea exposures, but the differences probably result from the higher temperatures present in the upper layers of the sea. As such rates measured in the laboratory have been shown to be uninfluenced by cell sedimentation in unshaken bottles, the limitation of rates measured in field experiments by this factor is very unlikely. At lower light intensities the gradients of the rate-intensity

relationship agree between both types of exposure. This similarity, with the small differences between the light-saturated rates, determines the correspondence betwen I_K values measured in laboratory and sea.

SOME PHOTOSYNTHETIC CHARACTERISTICS OF *CHAETOCERAS AFFINIS*

Although not the main object of these experiments, some descriptive information was accumulated on the photosynthetic characteristics of the diatom used. It is discussed below in relation to the few other comparable data which are available for the ecologically important algae of the marine and freshwater plankton.

The onset of light saturation of photosynthesis in relation to light intensity is an important determinant of the depth-distribution of photosynthetic rates; it can be characterized by a single intensity the I_K value. Its variation in natural populations of phytoplankton is poorly understood, but includes the effects of a pronounced, though often neglected temperature dependence. The present laboratory experiments yield I_K values between 4,600 and 7,700 lux, or an estimated equivalent of 19–32 kerg/cm^2 sec, at 14–16·5°C. The results of the sea experiments are similar but involve a greater temperature range. Wider comparison is often difficult, as other work with planktonic algae has frequently involved light fields with different spectral qualities and the use of different instruments or means of calculation for estimating light intensities. There is a general similarity with the values indicated for planktonic algae, particularly diatoms, at comparable temperatures (*e.g.* Jenkin 1937, Sagromsky 1943, Ryther 1956, Talling 1957a). The most conspicuous divergencies are shown by the high saturation intensities obtained for the surface phytoplankton of tropical oceans by Steemann Nielsen (1952) and Steemann Nielsen and Jensen (1957), using fluorescent illumination and an indirect means of assessing the effective light intensities.

The maximum photosynthetic capacity of a unit quantity of algae, measured under light-saturation, is another characteristic useful for analytical and comparative purposes. Three indices of algal quantity were used here: (i) cell numbers, (ii) cell volume, calculated from cell numbers and cell dimensions, and (iii) chlorophyll *a* content. The first is unsuitable as a general measure owing to the variation of cell size, which also contributed to changes of chlorophyll *a* content per cell. Contents measured for 11 healthy cultures grown at 5,400 lux varied from 1.0–3.6 mg chlorophyll $a/10_9$ cells; a single culture grown at 970 lux gave the highest value of 4.6 mg/10^9 cells. Rates based upon cell volume and particularly chlorophyll *a* content have been much used in other studies of phytoplankton photosynthesis and productivity, although the experimental conditions have often been ill-defined especially as regards media, temperature, and light-saturation. The present laboratory experiments, carried out at 14–16°C using adequately buffered media and cells grown at 5,400 lux, yield rates of 29–32 mg 0_2mg chlorophyll *a*/hour for the four longer experiments in which the initially lower rates can be eliminated (Figs. 1, 2 and 3). These values are much greater than those commonly reported for either cultured or natural populations of algae. Ryther and Yentsch (1957) have based a method of calculating photosynthetic production in the sea upon an average value of 3.7 g C/g chlorophyll *a*/hour, which is equivalent, using their value of 1.25 for the photosynthetic quotient, to 12.3 mg O_2/mg chlorophyll *a*/hour. The present experiments provide fewer data for rates based upon cell volume, owing to uncertainties in estimating volume for geometrically complex cells. The values obtained from two laboratory experiments, under the conditions listed above, are 0.048 and 0.073 mg 0_2/mm^3/hour; in the first figure the effect of the initial 'lag' is eliminated. These rates are also higher than most values previously published for natural populations of phytoplankton (Verduin 1956), although higher values are not unknown (Talling 1957c).

Little is known concerning the variation of photosynthetic behavior between cells with different histories, which can be im-

portant in other algae (*e.g.* Sorokin 1958). An experiment already described (Fig. 3) compared the behavior of cells grown at a low light intensity of 970 lux with that of cells grown at a higher intensity of 5,400 lux and then kept in darkness for two days. These differing pre-treatments had little effect on the I_K characteristic, but light-saturated rates of photosynthesis were lower in cells cultured at the lower intensity whether expressed in terms of cell numbers, cell volume, or chlorophyll *a* content. The relatively vigorous activity of cells after two days in darkness is ecologically significant, as such dark conditions must often befall cells circulating in nature. A similar response has been obtained with a freshwater plankton diatom (Talling 1957a).

DISCUSSION

Most of the numerous recent measurements of photosynthesis of phytoplankton populations have involved attempts to duplicate, in field experiments, conditions prevailing in a natural water-body during a certain time. As even the field experiments described here involve simplified conditions, such as uniform algal material and short exposures, many factors affecting the populations in nature are not represented. Examples include the possible differentiation of photosynthetic capacities between cells circulating at various depths or photosynthesising at different times of the day. Nevertheless such simplification allows a better resolution of many important factors and permits direct tests of the application of laboratory data to field conditions.

Within these limits, the results generally support the value of measurements based on exposures in closed bottles even when, as in field experiments, effective shaking of the cell suspensions is not possible. The conditions controlling the appearance of secondary effects during long exposures (*cf.* also Ryther and Vaccaro 1954, Vollenweider 1956, Bauer 1957, Rodhe 1958) are not explored, but the photosynthetic rates were shown to be well maintained in exposures of up to three hours. They appeared only slightly modified by lower initial rates, in which induction phenomena were presumably involved. The effectiveness of the method of following photosynthesis by the Winkler oxygen estimation is particularly noteworthy in view of the relatively high algal densities and photosynthetic rates involved. It has been suggested (Steemann Nielsen and Jensen 1957) that uptake of iodine by unsaturated algal constituents may render the Winkler method unusable with dense algal populations. This consequence is not shown in the present experiments or many others described in the literature. The measurements here also show no indications of ill-effects due to the supersaturation with oxygen which resulted from high photosynthetic rates. Similar results were obtained by Vinberg (1934), using the Winkler method with freshwater phytoplankton. In general a marked supersaturation is undesirable, due to its possible effects on bubble-formation and rates of respiration (Gessner and Pannier 1958a,b). Recent unpublished work by the author demonstrates that the Winkler oxygen determination can also be used to detect photosynthetic changes as low as 0.02 mg/L, about two orders of magnitude lower than the changes involved in the present experiments.

Experiments which combine both laboratory and field exposures have relevance for the various recent attempts to use laboratory data for estimating photosynthetic productivity in nature (Ryther 1956, Ryther and Yentsch 1957, Rodhe, Vollenweider and Nauwerck 1958, Cushing 1958). A principal difficulty here is the comparison of light intensities measured in the two situations, particularly in view of the progressive spectral modification of underwater light with depth, which cannot be reproduced by a single color filter as used by Cushing (1957, 1958). A full comparison would require evaluation of the effects of differing qualities of vector and spectral distribution of radiation in laboratory and sea, the latter considered in relation to the action-spectrum of photosynthesis. The present assessment of effective light intensities, by the total energy flux of photosynthetically active radiation, is only an approximation but has value for interpreting field experiments under different conditions. Here it has given

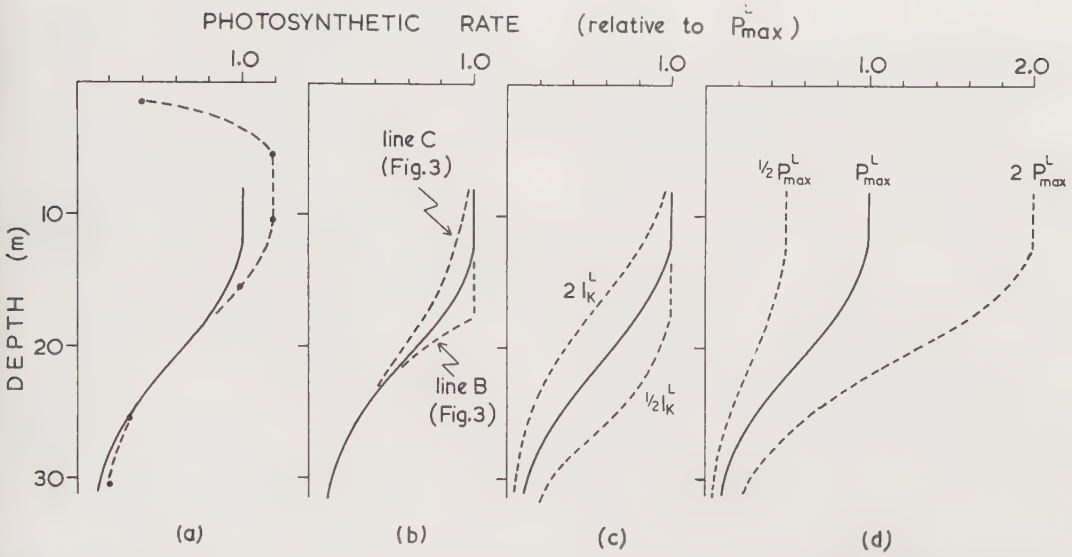

FIG. 7. The depth distribution of photosynthetic rate (full lines) calculated from the laboratory rate–light intensity curve, and the intensity–depth curve, for 5 Aug., 1957. With this depth distribution are compared (a) the photosynthetic rates measured *in situ*, (b) the depth distribution of rates calculated from two variants of the rate–intensity curve (see Fig. 4), (c) the depth distributions calculated for given changes in the I_K characteristic, and (d) for the same changes in the P_{max} characteristic. All photosynthetic rates are expressed relative to the laboratory value at light saturation ($P_{max}{}^L$).

general agreement between rate-intensity characteristics of photosynthesis measured in the laboratory and at sea, so providing some support for the use of such laboratory data in calculating the vertical distribution of photosynthetic rates in nature. Such a calculation is illustrated in Figure 7. Because of the approximations involved, the agreement should be regarded as a working correlation rather than the outcome of a physically and physiologically adequate comparison. However, the type of calculation appears more complete than that involved in any previous comparison of laboratory and field experiments with planktonic algae. Thus the correlative relationship established by Steemann Nielsen (1952) does not include a direct comparison of specific light intensities or their effects. Ryther (1956) has described and compared rate-intensity characteristics of photosynthesis measured in the sea and in sunlight reduced by graded neutral filters. His estimates of underwater light intensities in foot-candles are based upon a single vertical extinction coefficient expressing the diminution in the response of a photo-cell with depth, and suffer from limitations discussed by Lund and Talling (1957) and Strickland (1958).

For many ecological purposes, estimates are needed of the total photosynthetic production below unit area. This can be expressed by the area enclosed by a photosynthesis-depth profile, and can be related to the individual variables controlling the distribution of photosynthetic rate with depth (Talling 1957b). When this depth distribution includes a well-developed region with light-saturation, as illustrated in Figures 5 and 6, it can easily be shown (Fig. 7) that the area mentioned is much more sensitive to variation in the maximum rate (P_{max}) than to similar variation in the onset of light-saturation (expressed by I_K). This feature is expressed in the equations derived by Talling (1957b) to relate the areal production to the P_{max} and I_K variables. With these conditions the experimental errors in determining I_K are less significant than errors in P_{max}, for which measurement of light intensity is not required. The obvious uncertainties in the measurement of I_K, therefore, are unlikely to affect strongly the final calculation of areal production.

Errors or uncertainties in the measurement of I_K, or of the initial gradient of the rate-intensity relation, will tend to become more serious in this connection when the surface intensity (I_o) is low and approaches I_K, and photosynthesis decreases rapidly with depth from the water surface. Another factor affecting the area under the photosynthesis-depth profile, and hence the areal production, is the intrinsic curvature of the rate-intensity curve. However when the effects of the most extreme curvature types of Figure 4 were tested, using a graphical construction of photosynthesis-depth profiles, the changes induced were small (Fig. 7b).

On present knowledge, field experiments involving exposures *in situ* still provide the most direct estimation of photosynthetic productivity by natural populations of phytoplankton. With suitable design, they can also allow the observed behavior to be interpreted in terms of a limited number of variables, from which photosynthetic behavior in other field situations can be estimated (Manning and Juday 1941, Edmondson 1956, Talling 1957a, b). The application of laboratory measurements involves still wider extrapolation, but has been used in recent work with radio-carbon in view of the saving of time and greater ease of measurement. Nevertheless the significance of the measurements is often uncertain, partly on purely physiological grounds such as the unknown effects of temperature on the P_{max} and I_K variables and the incomplete attainment of light-saturation, and partly from uncertainties from the widespread application of formulae (*e.g.* those of Steemann Nielsen 1952, p. 132; Ryther 1956, Ryther and Yentsch 1957) without sufficient testing of the validity of the basic assumptions for local conditions. Other attempts to simplify field conditions of exposure, using photosynthetic rates measured only near the water surface, are still more unsatisfactory in view of the unknown significance of photo-inhibition in such exposures. A need exists for the greater development of analytical studies of photosynthetic productivity by phytoplankton, broadly based upon both laboratory and field experiments, and involving short exposures under conditions better defined than in most previous field experiments.

REFERENCES

Anderson, E. R. 1952. Energy-budget studies. U.S. Geol. Surv., Circ. **229**: 71–119.

Bauer, G. 1957. Die Ausnützung der Sonnenergie durch das Phytoplankton eines eutrophen Sees. Inaugural-Dissertation, Universität München, 77 pp.

Cushing, D. H. 1957. Production of carbon in the sea. Nature, Lond., **179**: 876.

———. 1958. Some experiments using the ^{14}C technique. Rapp. Cons. Explor. Mer., **144**: 73–75.

Davis, F. J. 1941. Surface loss of solar and sky radiation by inland lakes. Trans. Wis. Acad. Sci., Arts & Lett., **33**: 83–93.

Edmondson, W. T. 1956. The relation of photosynthesis by phytoplankton to light in lakes. Ecology, **37**: 161–174.

Emerson, R. 1935. The effect of intense light upon the assimilatory mechanism of green plants, and its bearing on the carbon dioxide factor. Cold Spring Harbor Symp. Quant. Biol., **3**: 128–137.

——— and L. Green. 1934. Manometric measurements of photosynthesis in the marine alga *Gigartina*. J. Gen. Physiol., **17**: 817–843.

Gessner, F. 1955. Hydrobotanik. I. Energiehaushalt. Deutscher Verlag der Wissenschaften, Berlin, 517 pp.

——— and A. Diehl. 1951. Die Wirkung natürlicher Ultraviolettstrahlung auf die Chlorophyllzerstörung von Planktonalgen. Arch. Mikrobiol., **15**: 439–453.

——— and F. Pannier. 1958a. Der Sauerstoffverbrauch der Wasserpflanzen bei verschiedenen Sauerstoffspannungen. Hydrobiologia, **10**: 323–351.

———. 1958b. Influence of oxygen tension on respiration of phytoplankton. Limnol. Oceanogr., **3**: 478–480.

Jenkin, P. M. 1937. Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation of submarine illumination in the English Channel. J. Mar. Biol. Assoc., U.K., **22**: 301-343.

Jerlov, N. G. 1951. Optical studies of ocean waters. Rep. Swedish Deep-Sea Expd., **3**: 1–59.

Kok, B. 1956a. On the inhibition of photosynthesis by intense light. Biochim. Biophys. Acta, **21**: 234–244.

———. 1956b. Photosynthesis in flashing light. Biochim. Biophys. Acta, **21**: 245–248.

———. 1957. Report on some recent results at Wageningen. In: Gaffron, H. (ed.), Research in Photosynthesis, pp. 353–365. Interscience Publishers, New York. xiv + 524 pp.

Levring, T. 1947. Submarine daylight and the photosynthesis of marine algae. Goteborgs

VetenskSamh. Handl., Sjatte Folj. B, **5**(6): 1–90.

LUND, J. W. G., AND J. F. TALLING. 1957. Botanical limnological methods with special reference to the algae. Bot. Rev., **23**: 489–583.

MANNING, W. H., AND R. E. JUDAY. 1941. The chlorophyll content and productivity of some lakes in north-eastern Wisconsin. Trans. Wis. Acad. Sci., Arts & Lett., **31**: 377–410.

RABINOWITCH, E. I. 1951. Spectroscopy and fluorescence of photosynthetic pigments; Kinetics of photosynthesis. Photosynthesis and related processes, II, Part 1. Interscience Publ., New York. pp. xi + 603–1208.

———. 1956. Kinetics of photosynthesis (cont'd). Addenda to I and II, Part 1. Photosynthesis and related processes, II, Part 2. Interscience Publ., New York. pp. xvi + 1209–2088.

RICHARDS, F. A., AND T. G. THOMPSON. 1952. The estimation and characterisation of plankton populations by pigment analyses. II. A spectrophotometric method for the estimation of plankton pigments. J. Mar. Res., **11**: 156–172.

RODHE, W. 1958. The primary production in lakes: some results and restrictions of the ^{14}C method. Rapp. Cons. Explor. Mer, **144**: 122–128.

———, R. A. VOLLENWEIDER, AND A. NAUWERCK. 1958. The primary production and standing crop of phytoplankton. pp. 299–322. *In* 'Perspectives in marine biology,' ed. A. A. Buzzati-Traverso. Univ. of California Press, Berkeley. xvi + 621 pp.

RYTHER, J. 1956. Photosynthesis in the sea as a function of light intensity. Limnol. Oceanogr., **1**: 61–70.

——— AND R. F. VACCARO. 1954. A comparison of the oxygen and ^{14}C methods of measuring marine photosynthesis. J. Cons. Int. Explor. Mer, **20**: 25–34.

——— AND C. S. YENTSCH. 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. Oceanogr., **2**: 281–286.

SAGROMSKY, H. 1943. Die Bedeutung des Lichtfaktors für den Gaswechsel planktontischer Diatomeen und Chlorophyceen. Planta, **33**: 299–339.

SMITH, E. L. 1936. Photosynthesis in relation to light and carbon dioxide. Proc. Nat. Acad. Sci., Wash., **22**: 504–511.

SOROKIN, C. 1958. The effect of the past history of cells of *Chlorella* on their photosynthetic capacity. Physiol. Plant., **11**: 275–283.

STEEMANN NIELSEN, E. 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. J. Cons. Int. Explor. Mer, **18**: 117–140.

———. 1958. Experimental methods for measuring organic production in the sea. Rapp. Cons. Explor. Mer, **144**: 38–46.

——— AND E. A. JENSEN. 1957. Primary oceanic production. The autotrophic production of organic matter in the oceans. Scientific Results of the Danish Deep-Sea Expedition round the World 1950–52, Galathea Report I: 49–136. Copenhagen.

——— AND V. HANSEN. 1959. Light adaptation in marine phytoplankton populations and its interrelation with temperature. Physiol. Plant., **12**: 353–370.

STRICKLAND, J. D. H. 1958. Solar radiation penetrating the ocean. A review of requirements, data and methods of measurement, with particular reference to photosynthetic productivity. J. Fish. Res. Bd. Canada, **15**: 453–493.

SVERDRUP, H. U., M. W. JOHNSON AND R. H. FLEMING. 1942. The oceans, their physics, chemistry and general biology. Prentice-Hall, New York. x +1060 pp.

SWEENEY, B. M., AND HASTINGS, J. W. 1957. Characteristics of the diurnal rhythm of luminescence in *Gonyaulax polyedra*. J. Comp. Cell. Comp. Physiol., **49**: 115–128.

TALLING, J. F. 1957a. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. New Phytol., **56**: 29–50.

———. 1957b. The phytoplankton population as a compound photosynthetic system. New Phytol., **56**: 133–149.

———. 1957c. Diurnal changes of stratification and photosynthesis in some tropical African waters. Proc. R. Soc. B, **147**: 57–83.

TAYLOR, A. H., AND G. P. KERR. 1941. The distribution of energy in the visible spectrum of daylight. J. Opt. Soc. Amer., **31**: 3–8.

UTERMÖHL, H. 1936. Quantitative Methoden zur Untersuchung des Nannoplanktons. *In*: Aberhalden Handb. Biol. ArbMeth., **9**(2): 1879–1937.

VERDUIN, J. 1956. Energy fixation and utilization by natural communities in western Lake Erie. Ecology, **37**: 40–50.

VINBERG, G. G. 1934. Versuch zum Studium der Photosynthese und der Atmung des Seewassers. Zur Frage ueber Bilanz des organischen Stoffes. (Mitteilung I). (In Russian: German summary.) Arb. Limnol. Sta. Kossino, **18**: 5–24.

VOLLENWEIDER, R. A. 1956. Das Strahlungsklima des Lago Maggiore und seine Bedeutung für die Photosynthese des Phytoplanktons. Mem. Ist. Ital. Idrobiol. Marchi, **9**: 293–362.

WINOKUR, M. 1948. Photosynthesis relationships of *Chlorella* species. Amer. J. Bot., **35**: 207–214.

WITHROW, R. B., AND A. P. WITHROW. 1956. Generation, control, and measurement of visible and near-visible radiant energy. *In* Hollaender, A. (ed.), Radiation biology, vol. **3**. Visible and near-visible light, pp. 125–258. McGraw-Hill Co., New York, Toronto, London. viii + 765 pp.

THE SPREAD PLATE AS A METHOD FOR THE ENUMERATION OF MARINE BACTERIA[1,2]

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ABSTRACT

A comparison was made of agar plates spread with glass rods and poured agar plates for the enumeration of bacteria in the waters of Fisher's Island Sound, salinity 30‰. Spread plates were shown to be markedly superior. Highest counts were obtained by spreading, using rods treated with Desicote (a silicone solution) and incubating plates at 25°C, rather than at 16°C, and in air rather than in air with CO_2 content increased.

INTRODUCTION

For the enumeration of bacteria in marine waters, extensive use is made of the poured agar plate. The possibility that some organisms indigenous to waters at less than 20°C were killed by even short exposure to 45°C and might grow more promptly on the surface of an agar plate suggested a challenge of the pour plate enumeration against a spread plate technique. The variations in conditions commonly employed suggested also the comparison of the effect of incubation at different temperatures and in an atmosphere of increased CO_2.

METHODS AND MATERIALS

Water was obtained at various tidal conditions during the summer and fall of 1958, from one location at Latimer Reef, which is about 6 miles off the coast of Noank, Connecticut, and east of East Point, Fisher's Island, New York. Top samples were collected in sterile 500 ml wide-mouth reagent bottles. Samples were iced until examination at the laboratory, within 2 hours.

Preliminary studies with samples from Fisher's Island Sound showed that counts could be obtained using decimal dilutions of 10^{-1} to 10^{-4}. Dilution blanks (9 and 99 ml of sea water) were sterilized in the autoclave. Pipettes were 1.1 ml (milk) pipettes, sterilized in the oven, and stored in cans. The plating medium was that used at the Woods Hole Oceanographic Institute reported by ZoBell (1946) and had the following composition: sea water from the tap at the Noank Marine Research Laboratory (salinity about 30‰); peptone (Gelysate, Baltimore Biological Laboratory), 0.1%; glucose, 0.1%; K_2HPO_4, 0.005%; Bacto-agar (Digestive Ferments Company), 1.5%; final pH 7.6. It was necessary to filter through cheesecloth.

All "platings" were made in duplicate. For the pour plates, the melted agar was tempered at 45°C, then mixed with the sample or dilution. For the spread technique, about 15 ml was poured into plates prior to use. Dilutions were made so that deposition of 0.1 ml on the surface resulted in the desired dilution. Using a separate rod for each, the inoculum was spread evenly over the entire surface of the agar by a rotary twirling motion of the plate under the rod. The rods were made of 5 mm Pyrex, formed into a spreading portion with handle as follows: a 90° bend was made near the center of a 25 cm length, about 2 cm from which another 90° bend was made, thus producing a crank with parallel but opposite legs; a third "upward" bend gave a spreading portion about 8.0 cm in length. The rods were oven-sterilized and stored in cans.

Pour plates were incubated at 16°±1°C; the spread plates at 16°±1°C and 25°±1°C. The lower temperature was chosen to approximate that of the waters sampled, while the 25°C is the upper limit suggested by ZoBell (1954). For incubation in an atmosphere of increased CO_2, the plates were in-

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TABLE 1. *Comparison of colony counts ($\times 10^2$) obtained by spread and pour plates at 16°C incubated in air and in air with CO_2*

Sample No.	Date and Tide	Air		Ratios S/P	Air with CO_2		Ratio S/P	Ratios of counts	
		Spread (S)	Pour (P)		Spread	Pour		S air/S CO_2	P air/P CO_2
1	7/17 Flood	26	14	1.8	23	20	1.2	1.1	0.71
2	7/25 Ebb	53	12	4.4	41	23	1.8	1.3	0.52
3	7/31 Ebb	11	2	5.5	19	2	9.5	0.58	1.0
4	8/7 Low	140	77	1.8	86	51	1.7	1.6	1.5
5	8/14 High	11	3	3.7	7	6	1.2	1.6	0.5
6	8/21 Flood	150	64	2.4	130	99	1.3	1.2	0.65
7	8/28 High	8	2	4.0	11	3	3.7	0.73	0.67
8	9/4 Flood	35	12	2.9	41	31	1.3	0.86	0.39
9	9/10 High	8	5	1.6	5	2	2.5	1.6	2.5
10	9/19 Ebb	190	120	1.6	110	100	1.1	1.7	1.2
		Average ratios		2.9			2.5	1.2	0.96

Average ratio of spread:pour in both air and CO_2: 2.74
Average ratio of air:CO_2 with spread and pour: 1.1

cubated in a wide mouth jar sealed after lighting a candle.

After 7 days of incubation, plates were counted with the methods of the American Public Health Association (1955); counts were computed from no fewer than 4 plates (2 dilutions) and in most cases 8 plates (4 dilutions). Prolonged incubation resulted in larger colonies, not appreciably higher counts.

When spread plates appeared superior, a brief study was made to estimate the number of organisms recoverable from the rods following spreading. Several used rods were washed in 10 ml of sterile sea water, and the washings were plated by the spread method. Each rod showed a count of about 300. An appraisal was made of the practical value of Desicote, a silicone solution marketed by the Beckman Instrument Company, in order to obviate adherence of the water film entrapping bacterial cells. Treatment of the spreading rods consisted of dipping them in Desicote and shaking vigorously to remove excess. The treated rods were then sterilized as usual and used for spreading additional samples.

RESULTS AND DISCUSSION

In contrast to the findings of Carlucci and Pramer (1957), the spread plates always revealed higher counts, although the two sets of data are not strictly comparable. Table 1 shows that at 16°C, in air and in air with increased CO_2, the spread plates in all cases resulted in higher counts; the average of the ratios of counts, spread:pour, was 2.5 (range 1.1 to 9.5). Incubation of spread plates in air was in general superior to

TABLE 2. *Comparison of colony counts (× 10^2) of plates spread with Desicoted and plain rods incubated in air and in air with CO_2*

Sample No.	Date and Tide	16°C				Ratio of counts 16°C				25°C				Ratio of counts 25°C				Ratio of counts 25°C/16°C			
		Air		CO_2		Air D/P	CO_2 D/P	D Air/ CO_2	P Air/ CO_2	Air		CO_2		Air D/P	CO_2 D/P	D Air/ CO_2	P Air/ CO_2	D Air	D CO_2	P Air	P CO_2
		D°	P°	D	P					D	P	D	P								
14	10/25 Flood	13	8	7	6	1.6	1.2	1.9	1.3	20	12	12	10	1.7	1.2	1.7	1.2	1.5	1.7	1.5	1.7
15	11/1 High	12	9	8	6	1.3	1.3	1.5	1.5	18	18	7	15	1.0	0.47	2.6	1.2	1.5	0.88	2.0	2.5
16	11/8 Low	190	240	300	240	0.79	1.3	0.63	1.0	470	700	260	240	0.67	1.1	1.8	2.9	2.5	0.87	2.9	1.0
17	11/15 Ebb	46	29	9	16	1.6	0.56	5.1	1.8	48	35	14	14	1.4	1.0	3.4	2.5	1.0	1.6	1.2	0.88
18	12/6 Low	1300	1130	390	290	1.2	1.3	3.3	3.9	730	860	120	190	0.85	0.63	6.1	4.5	0.56	0.38	0.76	0.66
						1.3	1.1	2.5	1.9					1.1	0.88	3.1	2.5	1.4	1.1	1.7	1.3

Average ratio of D/P at all conditions: 1.1
Average ratio of air/CO_2 at all conditions: 2.5
Average ratio of 25°C/16°C at all conditions: 1.4
° Desicoted rod: D
° Plain rod: P

incubation in added CO_2 as shown by counts and by ratios (average ratio 1.2). With pour plates, incubation in CO_2 was superior, although with smaller differences in plate counts (average ratio 0.96).

Table 2 shows plate counts and ratios obtained with Desicoted and plain rods at two incubation temperatures both in air and in an atmosphere of increased CO_2. With cultures in air, it was observed that at both 16°C and 25°C, slightly higher counts were generally obtained by spreading with Desicoted rods (average ratios, 1.3 and 1.1); with plates incubated in CO_2 at both temperatures, the counts were generally not affected by the use of treated rods. The average ratio of all counts observed at all conditions, Desicoted:plain rods, was 1.1. Incubation in air is seen to be superior at both temperatures, whether the inoculum was spread with Desicoted or plain rods (average of all ratios 2.5). Incubation of plates at 25°C was superior to that at 16°C whether spread with treated or plain rods, in air or in air with increased CO_2 (average ratio 1.4). For other cooler or warmer waters, alternative incubation temperatures might be superior.

In comparing approximately 100 plates each of spread:pour, it was found that the reproducibility of counts obtained by the spread method was equal to that of the pour plate. There were apparently no unusual cultures obtained by this spread method as indicated by incomplete studies of several hundred strains. While spreading requires opening the plate, no excessive aerial contaminants were encountered even in our crowded laboratory.

REFERENCES

APHA, AWWA AND FSIWA. 1955. Standard methods for the examination of water, sewage, and industrial wastes. Tenth ed. APHA, Inc. New York. 522 pp.

CARLUCCI, A. F., AND PRAMER, D. 1957. Factors influencing the plate method for determining abundance of bacteria in sea water. Proc. Soc. Exptl. Biol. Med., **96**: 392–394.

ZOBELL, C. E. 1946. Marine microbiology. Chronican Botanica Co., Waltham Mass. 240 pp.

ZOBELL, C. E. 1954. Bacteriology of the sea. pp. 503–516. *In* Salle, A. J., Fundamental principles of bacteriology. McGraw-Hill Book Co., Inc. New York. 782 pp.

WATER TRANSPORT STUDIES IN THE STRAITS OF MACKINAC REGION OF LAKE HURON[1]

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ABSTRACT

The Straits of Mackinac comprise five simple straits in the region embracing Mackinac Island, Round Island, Bois Blanc Island, and the adjacent portions of the Upper and Lower Peninsulas of Michigan. Here the inflows from Lakes Michigan and Superior enter Lake Huron. Direct assessments of the inflow from Lake Michigan and of the run-off from the Lake Huron watershed, hitherto obtainable only by indirect means, have been made. The study indicates that large volumes of water move horizontally in oscillatory motion, due to the action of the Lake Michigan–Lake Huron uninodal seiche, but that this motion has no net effect upon the flow-through of waters from the upper lakes through Lake Huron. The excess of oscillatory transport over net flow-through indicates the seiche has an amplitude of about 0.1 m, a value which is independently confirmed by data from the literature.

INTRODUCTION

The Straits of Mackinac present the physical limnologist with a challenging complex of phenomena. A simple strait can be a puzzling problem; the Straits present a multiple condition in which component simple straits lie between the Upper and Lower Peninsulas of Michigan, between the Upper Peninsula and Mackinac Island, between Mackinac Island and Round Island, between Round Island and Bois Blanc Island, and between Bois Blanc Island and the Lower Peninsula (Fig. 1). Situated at the junction of Lake Michigan and Lake Huron, the Straits serve as an outlet for Lake Michigan, but their function in this capacity is complicated by the winds and seiches of the two lakes. Just east of the Straits, Lake Huron receives the inflow from Lake Superior through the St. Marys River. The complexity of the region makes it a difficult one to study, but its hydrographic importance as the origin of the major flow through Lake Huron renders it of real interest. Our original purpose in these studies was to test the dynamic height method of volume-transport determination in a complex area; that other and probably more important results could be obtained became evident as the studies went on.

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METHODS

The essential methods were the synoptic survey followed by computations of volume transport by the dynamic height method, with subsequent checking of current velocities by submerged current drogues.

Dynamic height computations of volume transport through the two transects adjoining Bois Blanc Island, in Mississagi Strait, and in the Manitoulin-Hammond Bay transect were made by the method described by Ayers (1956) and Ayers and Bachmann (1957). All these transects involved shoal water at their ends and the computations were carried out twice, being independently computed using the Helland-Hansen (1934) and Groen (1948) techniques for dynamic height computations in shallow water.

On 17 August 1956, after predominantly westerly winds of ten days duration, two vessels undertook a synoptic survey of the roughly polygonal area designated "Study Area" in Figure 1. One vessel made two transects at the level of the eastern end of

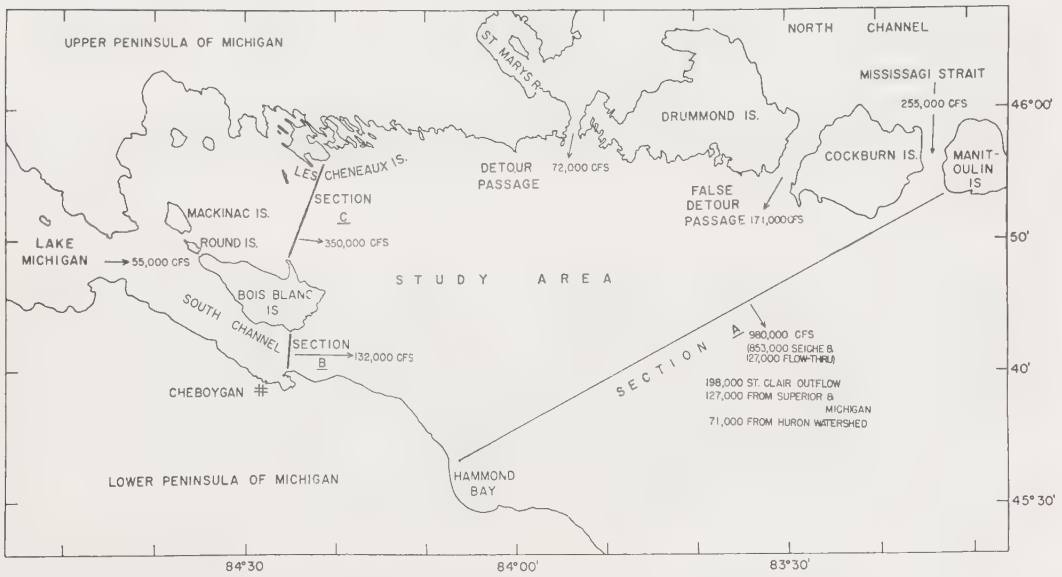

FIG. 1. Chart showing the "Study Area" and surrounding regions.

Bois Blanc Island. The second covered Detour Passage, False Detour Passage, Mississagi Strait, and then ran a long transect from Manitoulin Island to Hammond Bay on the Lower Peninsula.

The first vessel completed its transects, B and C, sufficiently early in the day for its results to be free of the effects of a southeast wind which appeared in the late afternoon. The second boat was about three-quarters through its section from Manitoulin to Hammond Bay when this wind began.

TABLE 1. *Volume transports into and out of the Study Area, cubic feet per second*

	Groen	Helland-Hansen	Mean
In:			
by dynamic computation			
Transects B and C	508,000	456,000	482,000
Mississagi Strait	279,000	230,000	255,000
by gauging			
Detour Passage	—	—	72,000
by current meter			
False Detour Passage	—	—	171,000
		Total in	980,000
Out:			
by dynamic computation			
Transect A	655,000	812,000	734,000
		Excess in	246,000

Volume transports in False Detour Passage were determined from current meter readings at each meter of depth. It had been planned to make similar current meter measurements in Detour Passage and in Mississagi Strait, but heavy steamship traffic in Detour and excessive depths in Mississagi made the necessary mid-channel anchoring impossible. Volume transport through Detour Passage is based on the U.S. Lake Survey's gaugings of the St. Marys River at Sault Ste. Marie, Michigan. This figure and the outflows of the St. Clair River at the foot of Lake Huron used later were kindly provided by Mr. W. T. Laidley of the U.S. Lake Survey (personal communication).

RESULTS

The volume transport figures obtained from all methods are given in Table 1. "In" and "out" refer to net transports into and out of the study area.

We do not pretend that steady-state conditions prevailed during the entirety of our synoptic coverage of the study area. The southeast wind of the afternoon of 17 August reached Beaufort force 3 and westward currents were found in the southern end of

transect A which was being covered at the time of this wind. Ayers *et al.* (1956, Figs. 18, 33, and 48) indicate that currents along the Hammond Bay shore are eastward under winds from westerly quarters.

There is every reason to believe, however, that the volume transports obtained for transects B and C, Detour Passage, False Detour Passage, and Mississagi Strait were free of effects of the southeast wind by virtue of being taken hours prior to the onset of the wind. We therefore consider that a balanced condition obtaining before the rise of the wind can be represented by the condition in which transports into and out of the study area are equal and that the mean value of inflow, 980,000 cfs, probably best represents the balanced-state outflow through transect A.

A volume transport figure of nearly a million cfs in the head of Lake Huron at a time when the outflow through the St. Clair River at its foot was 198,000 cfs could indicate either that volume transports determined by the dynamic height method were drastically in error, or that steady-state conditions in the ordinary sense did not apply at the time of our survey. That the latter was the case and that dynamic height computations are fairly accurate in the Straits region is indicated by the good agreement between surface velocity by dynamics and by drift bottles obtained by Ayers *et al.* (1956, pp. 28 and 60) at their 90-series stations in this region. Volume transport by dynamic computation in False Detour Passage on the day of the survey gave order-of-magnitude agreement with that obtained by current meter (93,000 to 171,000). On 25 July 1957, after a westerly wind regime comparable to that prior to the synoptic study, two current drogues set at the location of transect C gave 8.6 cm/sec east at 1 m and 1.1 cm/sec east at 50 m; these compare with 7.9 cm/sec east computed by dynamics at 1 m and 1.0 cm/sec computed by dynamics at 50 m, computations being based on data from the synoptic study.

On 6 August 1956, after westerly winds, two drogues were run at 4.6 and 13 m in South Channel near the location of transect B and compared to dynamic computations from simultaneous bathythermograph data. Drogue velocity at 4.6 m was 10.0 cm/sec and the computed velocity was 11.9 cm/sec, both southeast. At 13 m the drogue velocity was 11.5 cm/sec while that computed by dynamics was 1.1 cm/sec; no explanation can be given for the latter failure, but it was the only failure. All drogue studies were corrected by the method of Volkman *et al.* (1956).

The total complex of data indicates that our synoptic coverage of the study area, prior to the rise of the southeast wind, was under a temporary balanced-state condition in which transports into and out of the study area were equal, but in which a large volume of water was moving in seiche motion that would be expected to be oscillatory and to contribute nothing to the net downlake movement. Such a concept of a large volume of water in oscillatory motion in the area is not unrealistic. Computations of the Lake Michigan-Lake Huron seiches by Ayers and Ayers (unpublished) indicate that the Straits region contains a node of each seiche of the bi-lake system. Water movements at a node are horizontal. Location of a node in this region is borne out by the common knowledge that the Straits region is not one of common or extreme water-level changes, and that it is an area of strong and reversing currents.

The volumes of southward transport through False Detour and Mississagi Strait can be considered a normal result of the eastward passage of the seiche with subsequent development of height difference between North Channel and open Lake Huron. The velocities of flow computed for these passages were 36 and 28 cm/sec respectively, averaging 32 cm/sec. This average can be substituted into the formula for the speed of efflux of fluid from an opening.

$$V = \sqrt{2gh}$$

and the hydraulic head, 0.5 cm, needed to produce this velocity, computed. North Channel is almost completely cut off from the St. Marys River and Detour Passage and is not an area of pronounced seiche activity; Young (1929) reported a semidiurnal tide of two-inch amplitude and seiches of

magnitudes less than this. The 0.5 cm level difference needed for the observed velocity is apparently reasonable for the region.

If the balanced-state outflow through transect A, 980,000 cfs, is taken to consist of 853,000 cfs in oscillatory seiche motion plus an actual flow-through of 127,000 cfs (sum of inflows from Lakes Michigan and Superior, discussed below) the amplitude of the two-lake uninodal seiche can be derived from the figures of Ayers and Ayers. Using the method of Defant (1918) they compute that 43 km^3 of water have to move horizontally through a section near False Detour and Mississagi Strait if the seiche is given an arbitrary one-meter amplitude at Port Huron and Chicago. Taking 51 hours as the approximate period of the bi-lake uninodal seiche, 43 km^3 of water will move through this section at 8×10^6 cfs. Proportionally, therefore, the amplitude at section A will be 0.1 m:

$$8 \times 10^6 : 0.853 \times 10^6 = 1 \text{ m} : 0.1 \text{ m}$$

Similar results were obtained using data of Ayers (1956). In a section across Lake Huron between Oscoda, Michigan, and Southampton, Ontario, he obtained by dynamic computation a net south transport of 473,000 cfs. The gauged discharge of the St. Clair River at that time was 216,000 cfs. Assuming that the difference, 257,000 cfs, between the river discharge and the calculated transport represents water in oscillatory motion in the seiche, the amplitude of the bi-lake uninodal seiche can again be computed. With an arbitrary seiche amplitude of one meter, 22 km^3 of water must move horizontally through this section in 51 hours, giving a rate of flow of 4×10^6 cfs. Proportionating as before, the amplitude becomes 0.06 m:

$$4 \times 10^6 : 0.257 \times 10^6 = 1 \text{ m} : 0.06 \text{ m}$$

The results of these two calculations are in good agreement. The seiche is a very modest one, its small amplitude probably being the reason it has attracted no attention. The oscillatory water volumes appear reasonable.

An interesting, and possibly more important, aspect of these volume transport studies is that they have made possible a rough evaluation of the inflow into Lake Huron from its own watershed. On 6 August 1957 after westerly winds almost identical to those prior to the synoptic coverage of the study area, with normal bidirectional current, and with no unusual seiche activity evident, drogue studies to determine the outflow from Lake Michigan were carried out in the steamer channel west of the Mackinac Bridge. One drogue was set at 1 m; the other was at 36 m, well below the thermocline, the position of which was determined by bathythermograph. Prior to the setting of the drogues a bucket was lowered on a light line and the direction of its stray noted at each meter. Above the thermocline the bucket moved eastward, below it the direction of stray was west. Successive positions of the drogues were determined by sextant fixes on landmarks ashore. After several hours, when the drogues were so far separated that re-finding was difficult, they were taken up. The results, corrected according to Volkman *et al.* (1956), were: at 1 m, average velocity 14.9 cm/sec east; at 36 m, average velocity 11.4 cm/sec west. When multiplied by the cross-sectional areas above and below the thermocline, respectively, these values gave the following transports:

total east	113,000 cfs
total west	58,000 cfs
net flow	55,000 cfs east

Because of the pronounced similarity of meteorological and hydrographic conditions on 6 August 1957 and on the morning and early afternoon of 17 August 1956, when the study area was covered, it is reasonable to consider that the inflow from Lake Michigan was about the same. During the week of the study area coverage in 1956 the discharge of the St. Clair River was 198,000 cfs, while Lakes Michigan and Superior were delivering 55,000 plus 72,000 cfs for a total inflow of 127,000 cfs. The difference, 71,000 cfs, may be taken as the net contribution of the Lake Huron watershed. This can be independently computed as follows: for the years 1905–23 Horton and Grunsky (1927, Table 10) give the mean summer outflow of the St. Marys River through Detour Passage as 71,600 cfs, and of the St.

Clair River as 194,600 cfs. The difference between these figures, 123,000 cfs, is the mean combined contributions of Lakes Michigan and Huron. The inflow from Lake Michigan was reported by Judson (1909) as 57,000 cfs. Subtracting this from 123,000 cfs we obtain 67,000 cfs as an approximate mean contribution of Lake Huron, a good agreement with our present estimate of 71,000 cfs.

The original purpose of these studies, to test the dynamic heights method of determining volume transport in a complex area, appears to have been accomplished. But probably more significant is the at first-unexpected result that combined drogue and dynamic studies have produced a reasonable quantitative breakdown of the water movement in upper Lake Huron which can, at least in part, be checked.

REFERENCES

Ayers, J. C. 1956. A dynamic height method for the determination of currents in deep lakes. Limnol. Oceanogr., **1**: 150–161.

Ayers, J. C., and C. E. Ayers. Computations of the Lake Michigan-Lake Huron seiche (unpublished).

Ayers, J. C., and R. Bachmann. 1957. Simplified computations for the dynamic height method of current determination in lakes. Limnol. Oceanogr., **2**: 155–157.

Ayers, J. C., D. V. Anderson, D. C. Chandler, and G. H. Lauff. 1956. Currents and water masses of Lake Huron. Publ. No. **1** (Tech. Paper No. 1), Great Lakes Research Institute, University of Michigan, Ann Arbor, Michigan. Also, Res. Rpt. No. **35**, Div. of Research, Ontario Dept. Lands and Forests, Maple, Ontario. 101 pp., 47 figs., 4 tables.

Defant, A. 1918. Neue Methods zur Ermittlung der Eigenschwingungen (Seiches) von abgeschlossenen Watermassen (Seen, Buchten usw). Ann der Hydrog. w Meteor. **46**: 78–85.

Groen, P. 1948. Methods for estimating dynamic slopes and currents in shallow water. J. Mar. Res., **7**: 313–316.

Helland-Hansen, Bj. 1934. The Sognefjord section. pp. 257–274. *In* James Johnstone Memorial Volume. Univ. Press, Liverpool. 348 pp.

Horton, R. E., and C. E. Grunsky. 1927. Report of the Engineering Board of Review of the Sanitary District of Chicago on the lake lowering controversy and a program of remedial measures. Part III—Appendix II. Hydrology of the Great Lakes. The Sanitary District of Chicago, Chicago, Ill. xviii and 432 pp., 142 tables, 73 figs.

Judson, W. V. 1909. Currents in Lake Michigan. First Report of the Lake Michigan Water Commission, 1909, pp. 63–68. Urbana, Ill.

Volkman, G., J. Knauss, and A. Vine. 1956. The use of parachute drogues in the measurement of subsurface ocean currents. Trans. Amer. Geophys. Union **37**: 573–577.

Young, R. K. 1929. Tides and seiches on Lake Huron. Jour. Royal Astron. Soc. Canada, **23**: 445–455.

STUDIES OF THE NIANTIC RIVER, CONNECTICUT WITH SPECIAL REFERENCE TO THE BAY SCALLOP, *AEQUIPECTEN IRRADIANS*[1]

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ABSTRACT

The Niantic River is a shallow estuary with a tidal prism equal to half the mean low water volume of the basin, and with a twelve-hour freshwater inflow of less than 3% of the tidal prism. The tidal waters mix offshore with the waters of eastern Long Island Sound, rich in plankton and nutrients. The estuary functions as an ecological concentrating system as the dense and varied populations of grazers consuming the food of these tidal waters benefit from the resources of offshore mixing in addition to the production endemic to the estuary.

The disappearance of the eelgrass, *Zostera marina*, with the epidemic of the early 1930's permitted better circulation near the river bottom. Apparently this was advantageous to the bay scallop, which thereafter became the predominant sessile grazer with a production calculated at 2.2g C/m^2/yr. Anchorage previously offered by eelgrass for the early setting stages of scallops was subsequently available through the abundance of small branching algae.

The brief life history of a bay scallop is outlined on its shell as the surface laid down in each successive year appears rougher or more "weathered" than that formed the year before. By following this differentiation of shell surface, annual rings were determined with more certainty than in earlier studies. Though the time of year when the differentiation of shell surface commences may vary with populations and even with year classes, it is probably due to a common cause, seasonal change in growth rate being most likely. The life history interpreted from shells from Indian middens was essentially the same as observed for living scallops.

The scallops of the Niantic River spawn from mid-June through July. The young of a given year reach maturity and are the chief brood stock of the succeeding spawning season. Mortality rates for all sizes are high during all seasons and few individuals survive to the time of second spawning.

The estuaries in which the bay scallop occurs have the following hydrographic features: the ratio of tidal volume to river flow is high, thus the salinity remains high; the basin is relatively shallow, with a resulting high ratio of tidal volume to the volume at low water; the circulation is such as to retain the planktonic scallop larvae in sufficient numbers for reseeding and to provide an adequate supply of planktonic food, perhaps in part supplied by offshore waters.

INTRODUCTION

Prior to the 1930's, the Niantic River in Connecticut supported a small little-noticed population of the bay scallop, *Aequipecten irradians*. In the thirties as the eelgrass, *Zostera*, disappeared scallops rapidly increased in number and gave rise to a significant local fishery which has persisted to this date. Occasional high yields from small parent populations are common for this species, but continuing high yields after a sudden increase as observed in the Niantic River constitutes an unusual pattern.

[1] Contribution No. 26 from the Narragansett Marine Laboratory.

The field work for this study was supported by the Waterford-East Lyme Escallop Commission. The courtesies extended to me as a visiting investigator at the Bingham Oceanographic Laboratory, Yale University, and the field facilities made available at my parent's residence on the Niantic River were also vital to the study program. Many individuals and groups helped, a few being mentioned where appropriate in the text. Support was received from Alfred University and its Research Foundation.

THE NIANTIC RIVER

The Niantic River (Fig. 1) is an estuary draining into Niantic Bay, a bight at the

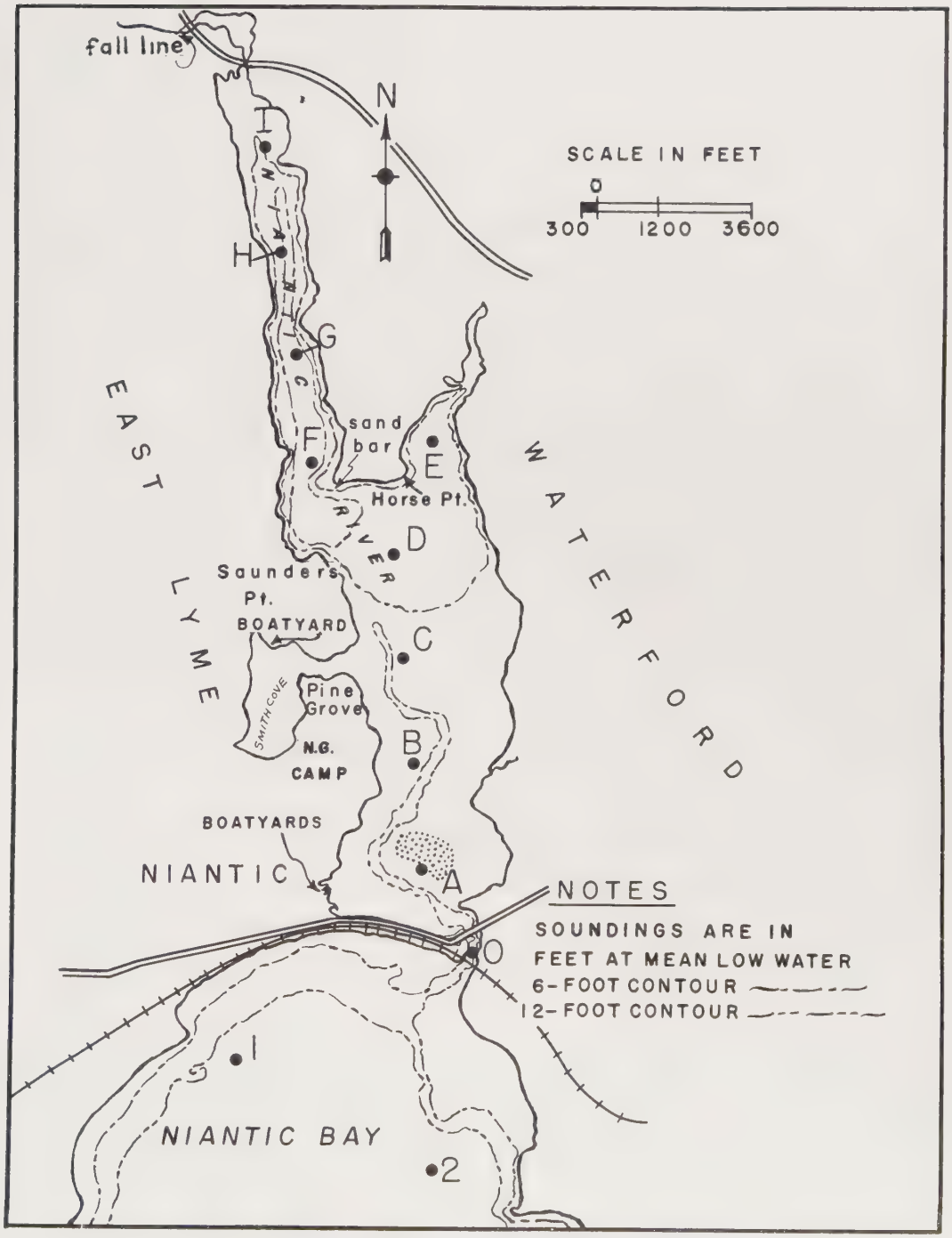

FIG. 1. The Niantic River, Connecticut, showing location of stations.

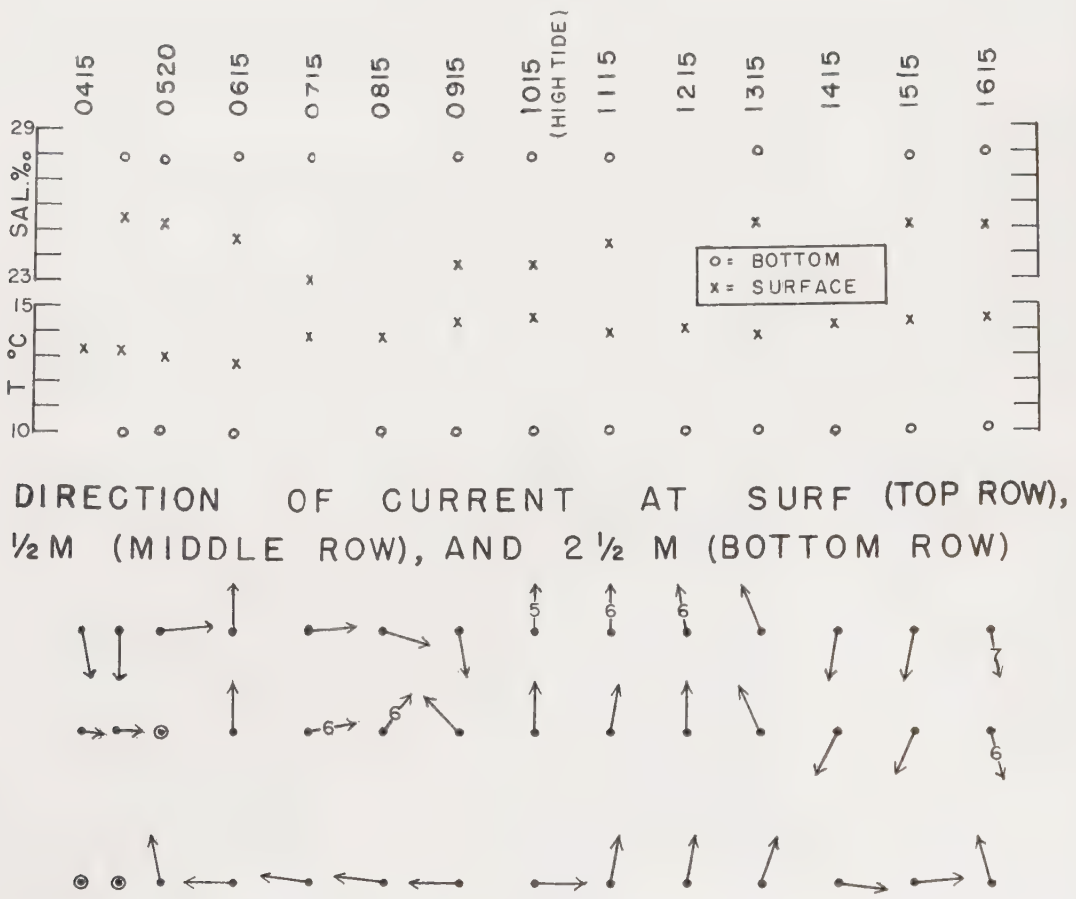

FIG. 2. Tidal cycle at Station D. There was a slight, dying breeze out of the NE when observations started. A gentle breeze came up out of the S at about 0915. This died at 1400 and was followed by a breeze from the W, and SW, and by 1530 from the NW. Temperatures were taken by max-min thermometer with the assumption that change progressed in a constant direction with depth. The depth to the bottom where salinity and temperature measurements were made ranged from 3½ m to 4¼ m according to the stage of the tide.

eastern end of Long Island Sound between the mouths of the Connecticut and Thames Rivers. The drainage area is about 30 square miles (Corps of Engineers 1945). The distance from the fall line of the main tributary to the mouth is about 3½ miles. The estuary is over half a mile wide through the lower stretches. Though depths between 8 and 20 ft prevail for most of the river, the last mile toward the mouth comprises sand flats partially exposed at extreme low tides. A meandering channel traverses

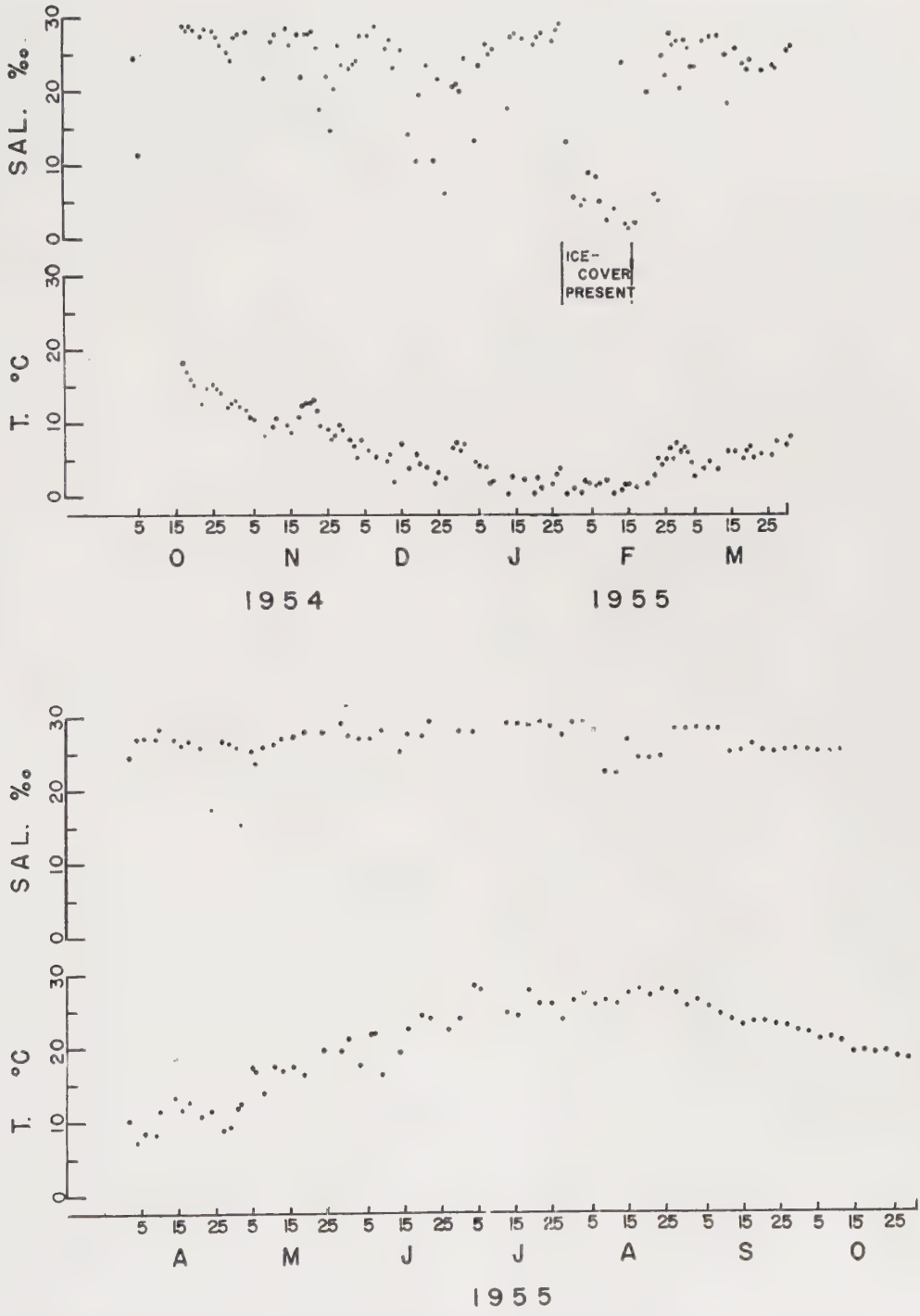

FIG. 3. Annual cycle of temperature and salinity at Saunders Point. At times of flat calm or of ice cover, appreciable temperature differences were noted as the bulb of the thermometer was raised or lowered a few inches near the surface.

these flats and makes a cut about 130 ft wide through a river-mouth sand bar.

Man's use of the Niantic River has done little to alter these waters. The highway and railroad running along the sand bar and across the inlet may tend to stabilize the river mouth; except for minor shifting of the inlet, the sand bar would probably be much the same under more natural conditions. Most of the drainage area is second-growth forest on farm and timber land. There is considerable clearing for houses along the shores. Wastes from these houses pass into individual septic tanks which serve effectively as indicated by a State Department of Health survey in the summer of 1954. *E. coli* counts did not exceed 100 per 100 ml, and almost every station received a top sanitary rating. The increasing traffic of pleasure boats with living accommodations may contaminate the river in the future if controls are not adequate.

The area of the Niantic River, plotted from a grid breakdown of the U.S. Coast and Geodetic Survey chart, is 3,196,800 m^2. The mean low water volume of the basin equals 5,287,200 m^3. The only available tidal range figure is the mean of 0.8 m given by the U.S.C.G.S. for Millstone Point, about a mile off the river mouth. Observations suggest this is a reasonable working figure applicable most anywhere in the estuary. The tidal prism based on such figures is 2,557,400 m^3 or about 50% of the mean low water volume.

In the lower river strong and direct ebb and flood tidal currents were observed (Table 1). The strongest currents were in the inlet where they were maximum in the middle of the ebb and flood phases of the cycle. In the deep waters upriver, tidal currents were slight (Table 1 and Fig. 2) with directions often modified by or subordinate to wind currents. Throughout the river very shallow currents unrelated to the main flow may develop quickly in response to the wind.

Figure 3 presents year around data on surface temperatures and salinities from a mid-river reference station at Saunders Point. Figure 2 and Table 2 give data on the horizontal and vertical gradients in these properties, the latter showing distinctly lower temperatures and higher salinities toward the bottom at stations upriver from the flats.

TABLE 1. *Observed currents in the Niantic River*
Measurements recorded for the surface were by drift bottle or by current cross floating just below the surface; deeper measurements were by current cross. All were taken from anchored skiff and were either ebb or flood as appropriate to the stage in the tidal cycle, except for two observations at Station F when the current flowed in the opposite direction with the wind. Currents too slow to be measured by this method are entered below as 0.

Station	No. of observations	Current velocity (cm/sec.)		
		Max.	Min.	Average
O[1]	4 at 0m	81	48	60.5
A	4 at 0m	38	5	21.2
B	4 at 0m	14	0	9.0
C	4 at 0m	6	0	2.5
D	34 at 0m	7	0	1.4
	18 at 2½m	0	0	0
E	5 at 0m	0	0	0
	3 at 2½m	0	0	0
F	6 at 0m	5	0	2.2
	4 at 2½m	0	0	0
G	5 at 0m	6	0	1.2
	3 at 2½m	0	0	0
H	4 at 0m	6	0	1.5
	1 at 2½m	0	0	0
I	4 at 0m	6	0	1.5

[1] Observations by the U. S. C. G. S. at this station July 29 and 30, 1929 (made available through correspondence with the Acting Director) include the following:
Ten foot current pole: strength of flood 67 cm/sec.; strength of ebb 67 cm/sec.
Price current meter at 7½ feet: strength of flood 106 cm/sec.; strength of ebb 68 cm/sec.
Price current meter at 12 feet: strength of flood 104 cm/sec.; strength of ebb 55 cm/sec.

An adequate understanding of the circulation of the Niantic River must take into account: (1) the extent to which the tidal waters mix with the residual waters of the basin, (2) the non-tidal circulation due to freshwater inflow, and (3) the degree to which the tidal waters of the estuary retain their identity as they ebb into the Niantic Bay and return to the river.

Over the tidal flats in the lower stretches of the estuary there is a thorough mixing of the water, whereas in the middle and upper reaches of the estuary the vertical gradients just mentioned occur. The inconclusive data concerning these gradients suggest a condition which resists free mixing but lacks the sudden density changes that

TABLE 2. *Records of temperature and salinity along the length of the Niantic River*
Temperatures by max-min thermometer. The readings entered for each depth are based on assumption that temperature change progressed in a constant direction with depth. Salinities by Harvey titration method.

Station	Depth meters	March 7, 1955				May 5, 1955				May 14, 1955[1]	
		Ebb		Flood		Flood		Ebb			
		°C	‰	°C	‰	°C	‰	°C	‰	°C	‰
2	0									11.9	28.2
	6									9.2[2]	28.7
1	0									12.2	28.1
	5									9.2[2]	28.7
0	0	2.6	29.1	2.5	28.9	10.0	27.7	11.1	27.7	14.7	27.3
A	0	3.3	28.5	2.8	28.1	9.9	28.0	11.9	27.8	14.7	27.1
B	0	3.3	27.4	2.9	27.9	11.2	27.2	15.1	26.7	15.6	27.0
C	0	3.3	27.3	2.5	27.7	13.9	26.0	15.7	25.9	15.6	26.8
D	0	4.2	27.2	2.4	18.9	16.6	22.8	16.9	24.7	16.1	26.7
	1									15.0	26.9
	2									13.6	27.7
	3	3.3[2]		3.3[2]	28.9	9.9[2]	27.9	9.6[2]	27.5	12.2	28.1[3]
E	0	2.8	26.2			15.6	18.1	18.3	20.0	15.8	26.6
	1									15.6	26.8
	2									13.3	27.0
	3	3.8[2]	28.1			10.6	27.8	10.0[2]	27.4	12.2	28.0
F	0	3.3	25.8			16.1	14.0	17.5	23.7	17.6	26.2
	1									14.6	26.8
	2									13.2	27.6
	3									11.7	28.0
	4									11.1	28.2
	5	4.4[2]	28.9			8.9[2]	27.7	9.0[2]	27.7		
G	0	2.2	15.4			16.4	7.7	17.8	23.5	17.4	24.4
	1									15.5	25.9
	2									12.8	27.6
	3									11.8	28.0
	4									11.2	27.8
	5	4.4[2]	29.1			8.9[2]	27.7	9.2[2]	27.5	11.1	28.2
H	0					16.7	10.6	18.8[2]	21.4	17.2	23.5
	1									15.6	25.5
	2							12.3	26.7	14.2	27.3
	3					9.9[2]	27.6				
I	0					17.2	11.2	19.6	9.9	18.3	20.6

[1] Stations 1 and 2 on ebb; 0 at slack; others on flood.
[2] These samples were taken just off the bottom a half meter or less from the depth indicated.
[3] Original salinity sample was broken and this is a substitute sample taken on the following flood.

would isolate deeper waters from those of the surface.

The non-tidal circulation due to freshwater inflow must be weak. Stream flow data are not available for the Niantic tributaries; however, for the similar neighboring watersheds Great Brook, the East Branch of Eightmile River, and the Menunketesuck River the average is 1.82 cfs per square mile[2] (U.S. Geological Survey 1954). Applying this figure to the Niantic tributaries, the freshwater inflow is estimated at 54.6 cfs or 67,000 m^3 during a tidal cycle. Such a tributary flow is less than 3% of the tidal prism.

Ketchum (1951) has provided a method

[2] Measured at Poquonock Bridge, near North Lyme, and near Clinton, respectively.

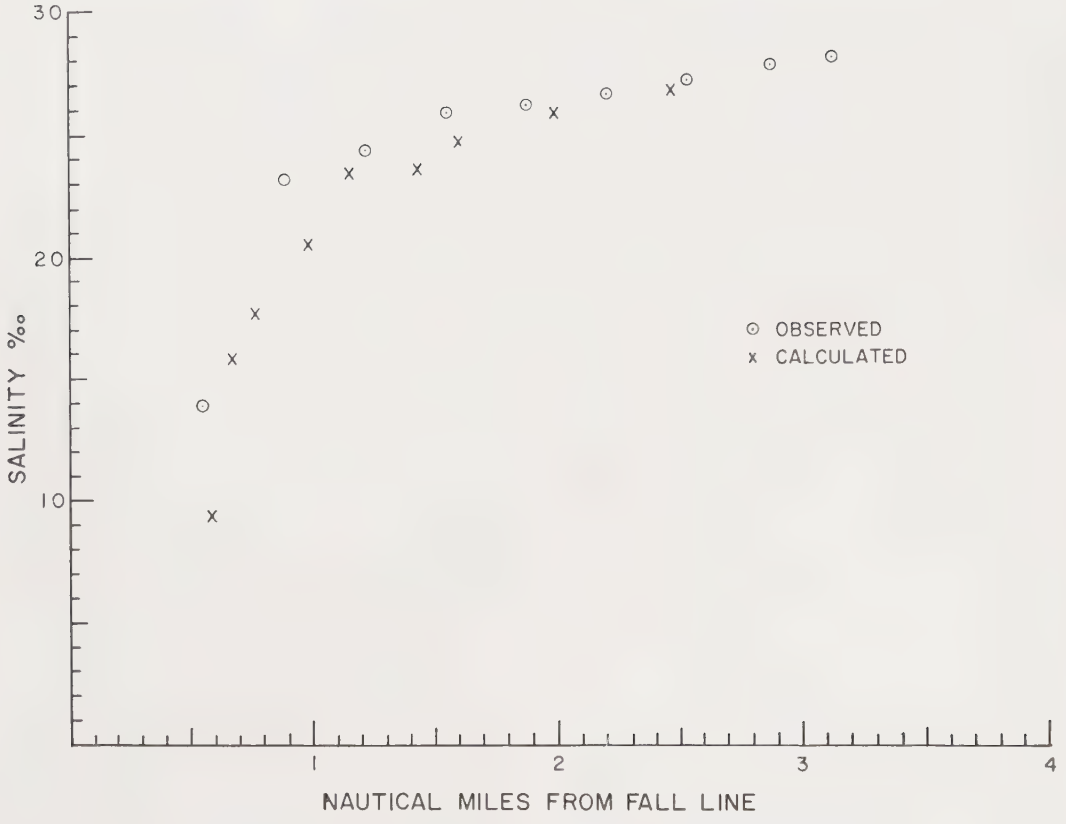

FIG. 4. Observed salinities in the Niantic River and those calculated by the method of Ketchum (1951).

for calculating the distribution of salinities within an estuary using measurements of the basin on U.S. Coast and Geodetic Survey charts plus two factors for which estimates are provided in this paper—the tidal range of 0.8 and the tributary discharge of 54.6 cfs. Figure 4 compares the calculated with the observed salinities. Since the curves match, the estimates of river flow and tidal range seem substantiated; furthermore, since these calculations do not allow for river stratification, the view that the deeper waters are seldom isolated is supported.

The degree to which the tidal waters retain their identity off the mouth of the river can only be discussed hypothetically. These waters ebb into Niantic Bay which appears to be a partially effective containing basin (some of the basin outline is shown in Fig. 1). Thus it is probable that the waters which ebb out of the estuary, though unbounded offshore and subject to dispersal and exchange with Long Island Sound waters, retain partial identity as a water mass flowing into and out of the river.

The sediments of the river, sampled every few hundred yards with a scoop, exhibit a simple relationship to hydrographic features. The deeper areas with little current have an accumulation of very fine and soft muds. Over the shallow flats and in the scoured channels downriver, sediments are of firm mixed sand and mud. The intertidal bottoms and the shallows near shore are also firm, with the sand content generally highest where wave and current action is greatest. Pebbles and small rocks are abundant in the sand along the shores. Almost everywhere the banks of the river are slightly elevated, and about one-fifth of the shoreline is of rock exposure.

Prior to the wasting disease which killed

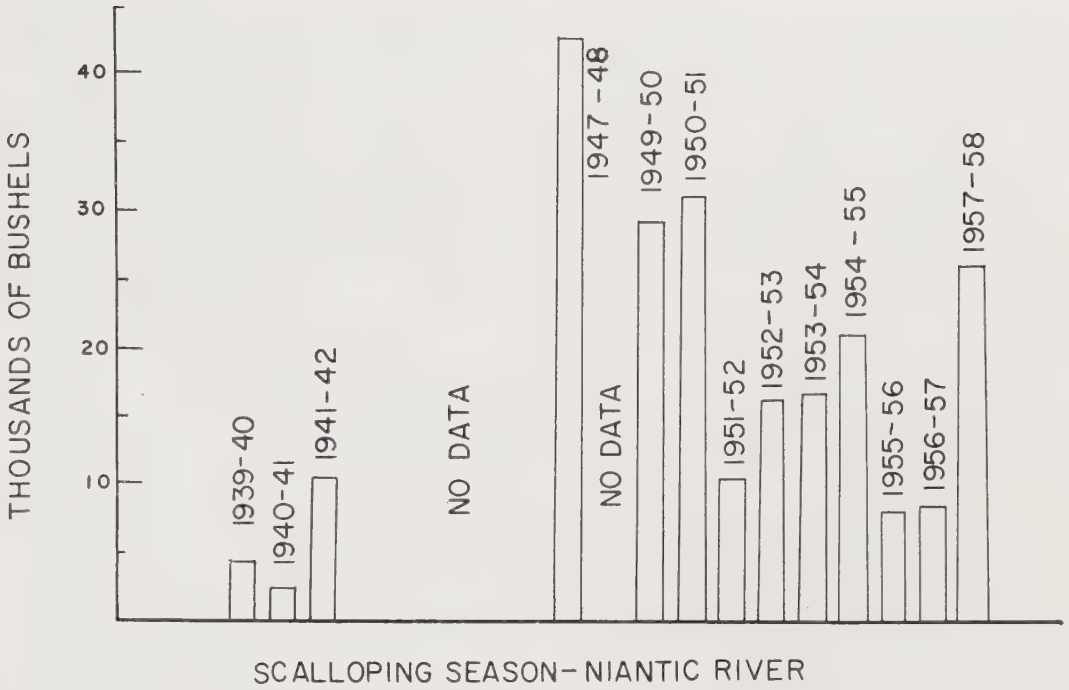

FIG. 5. Annual scallop harvest in the Niantic River according to permit sales.

off the eelgrass, *Zostera marina,* in the early 1930's, the river was so choked by the blades of this seaweed that neither rowing nor outboard travel was possible in the shallows at low tide.[3] The disease effected nearly complete destruction of *Zostera* by 1933, though after a few years the eelgrass began to return (see Cottam and Addy 1947, and Stevens *et al.* 1950 for summaries and references). Now at mid-summer some rather thick stands of *Zostera* are to be found in the Niantic River, particularly in a band about 600 yards wide extending across the river off the mouth of Smith Cove. Such stands, in the belt just described and elsewhere in shallow waters, do not reach the density of former growths; furthermore, the recovery seems very unstable, with large patches dying off from time to time. Several authors have mentioned recovery of the eelgrass along the coast, but in such reports the pattern is also inconsistent and suggests instability (Stevens *et al.* 1950).

[3] These are my own recollections from boyhood, substantiated by the comments of others who recall this condition.

On some bottom areas kelps were found, and along the shores there were occasional stands of *Ulva* or of rockweeds; however small branching red algae made up the bulk of the vegetation and were abundant almost everywhere except on bottoms swept clean by scouring currents.

HISTORY OF THE SCALLOP IN THE NIANTIC RIVER

There is little doubt that scallops are native to the Niantic River, for old-timers of the area tell of getting at least a few scallops as far back as they remember, and scallop shells are abundant in Indian middens in the vicinity.

In an earlier paper (Marshall 1947), I attempted to show that the local scallop population had been sparse and had suddenly increased to an abundance which supported a new fishery after the eelgrass disappeared. Doubts raised from the recollections of others as to just when the fishery developed prompted me to check the accounts of the early fishery in the archives of the *New London Day.* Write-ups of the fall of 1934

and in early 1935 emphasized the developing fishery. The new crop was being removed very rapidly by relatively few people, and there was mounting pressure to establish new controls to save and share the resource. Consistent with these accounts and the dates thereof is the legislation of 1935 establishing the Waterford-East Lyme Escallop Commission. Thus the association in time between the development of the scallop fishery and the disappearance of eelgrass in the early 1930's is well documented.

Figure 5 represents the scallop harvest by seasons. These totals are from the records of permits sold.[4] The permits limited the day's take according to the fee paid, with the maximum daily limit per person being three bushels. An analysis of permits for the 1954–55 scallop season showed that about two-thirds of the take was by men who fished for recreation or as a very incidental commercial effort. Well over half the take was in the first two months, October and November, of the six-month season. The take was primarily from the shallows downriver. Scallops are abundant elsewhere in the estuary and do well in the deeper water, though restrictions against the towing of gear has made it difficult to fish much beyond the shallows.

GROWTH AND LIFE SPAN OF BAY SCALLOP POPULATIONS

Of the length-frequency data gathered, those included in Figure 6 are the most representative. They portray a succession of samples taken from the middle of the river off Saunders Point where there was very little fishing.

Several procedures apply to these and all other samples of living scallops referred to in this study: (1) They were gathered with nets fine enough to collect the smallest scallops present. (2) Nets were towed, pushed and pulled, or handled in any manner that would expedite getting scallops. (3) There was no culling of samples, although an arbitrary unselected portion of a collection was sometimes used. (4) The size measurement used is the distance from the hinge to the far edge of the right valve as measured dorso-ventrally along the curvature of the shell. Other studies of scallops (notably Belding 1910 and Gutsell 1931) have dealt primarily with dorso-ventral height along a straight line tangential to the curvature of either valve. This is also the measurement commonly used for fishery regulations. The measurement along the curvature applied herein has the advantage of including size differences associated with thickness. When a flexible steel tape is used, quick and accurate measurements are possible and readings to shell markings such as growth rings can be taken directly from such a tape. For any given scallop the tangent measurement cannot be converted to that along the curvature, or *vice versa*; however, Figure 7 can be used for making conversions when comparing groups in which individual and condition differences average out.

The peak on the left in Figure 6, called the first peak hereafter, is clearly the 1954 age group, since there is no group of lesser size and since observations on reproduction and summer growth (reported below) leave no doubt that in the fall the young of a given year will approximate this size in November. Following the distribution graphs through the winter into spring and summer, the growth of this 1954 group is seen. Since the second peak, the one to the right, fades out in late spring and early summer, the graph suggests that this too is a single year class, that of 1953, affected by heavy mortalities by the end of its second year.

Figure 6 also provides a basis for interpreting a shell formation effect known as the growth ring, and supports the conclusion that the peaks of size-frequency represent age classes. Early shell growth, as observed for the 1954 year class in the fall collections, had a surface lustre which at its best appeared somewhat like a coat of varnish. Early in the spring these scallops developed a distinctly rougher surface at the periphery of their shells. As such coarser

[4] For years prior to 1952–53 it was necessary to estimate permit sales from cash received and any petty cash taken from receipts would make such estimates lower than actual sales. While some people do not take the full measure of it in permits, it is assumed that this is offset by the heaped bushels collected by others.

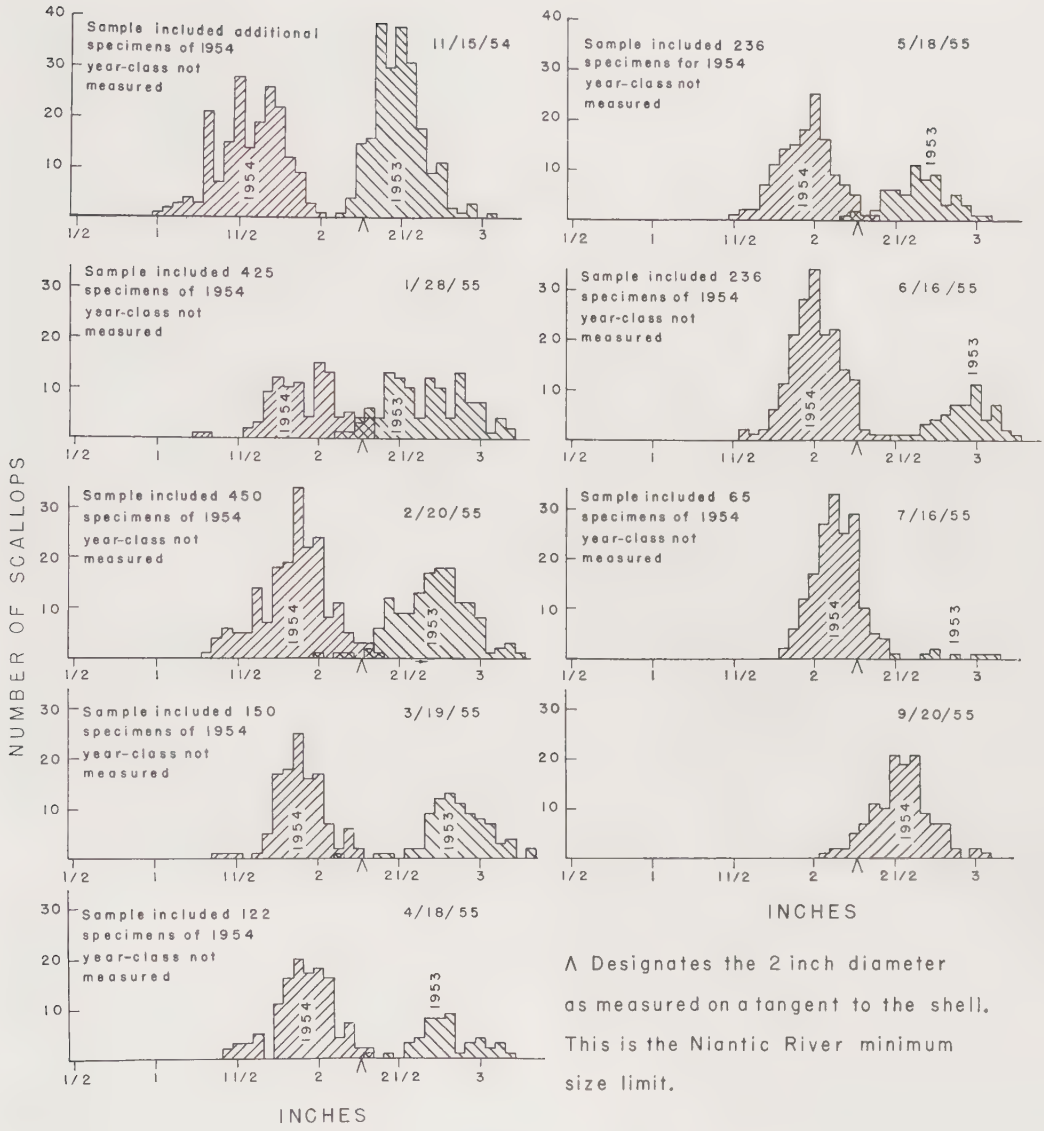
Sample included additional specimens of 1954 year-class not measured
11/15/54
Sample included 236 specimens for 1954 year-class not measured
5/18/55
Sample included 425 specimens of 1954 year-class not measured
1/28/55
Sample included 236 specimens of 1954 year-class not measured
6/16/55
Sample included 450 specimens of 1954 year-class not measured
2/20/55
Sample included 65 specimens of 1954 year-class not measured
7/16/55
Sample included 150 specimens of 1954 year-class not measured
3/19/55
9/20/55
Sample included 122 specimens of 1954 year-class not measured
4/18/55
1954
1953
NUMBER OF SCALLOPS
INCHES
INCHES
Λ Designates the 2 inch diameter as measured on a tangent to the shell. This is the Niantic River minimum size limit.
DISTANCE FROM HINGE TO EDGE OF RIGHT VALVE AS MEASURED ALONG CURVATURE

FIG. 6. Size–frequency distributions from sampling station in the middle of the Niantic River off Saunders Point.

shell was laid down (and this was first noted in the March 19 samples) a ring could be seen where the growth of the first winter had ended and that of the spring and the second summer had commenced. Following these criteria in the older group, the second peak, one finds a third differentiation of rougher appearance. This did not form a band sufficient to show a clear growth ring except on the few scallops that survived for an appreciable growth into their third summer. To the practiced eye the difference in the shell surface makes it possible to distinguish between annual growth rings and numerous other concentric rings on the shell.

The distance to the first growth ring on the 1953 year class, as determined from 144 second-year scallops collected from the mid-

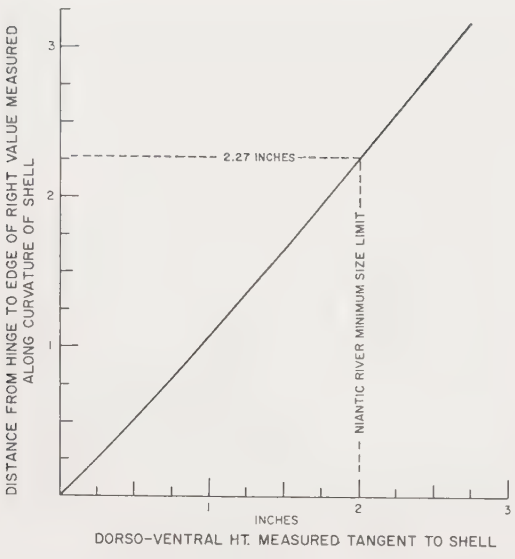

FIG. 7. Tangent height compared to distance as measured along the curvature of the shell. Line is drawn by sight from measurements on 159 scallops.

river station, was 1 1/16 inches. This is about the size attained by 1954 specimens at this station late in the winter (Fig. 6) when the growth ring formed, so it may be assumed that the ring formation resulted from the same cause and at the same season in both year classes. The pattern may vary, however, for in a sample of 293 specimens of the 1957 year class, taken on June 21, 1958, the growth beyond the ring was just becoming noticeable and apparently had not started until late spring.

The practical test of such a growth and age indicator comes through use. Until shell surface differentiation was taken as a criterion, some markings were incorrectly recorded as annual rings and others were missed. When frequency peaks overlapped, it was impossible to differentiate with certainty between rapidly-growing younger specimens and retarded scallops of the older group. The use of surface texture eliminates such ambiguities.

Belding (1910) working in Massachusetts did not stress the differentiation of shell surface as a mark of age. In discussing the annual growth ring, he stated that it was sometimes obscure and sometimes difficult to distinguish from other concentric shell markings. The growth line which he observed marked the onset of the spring growth; however, his view that it followed a period of "no growth" from November to May could be an exaggeration based on temperature effects on confined scallops. Gutsell (1931), working with the populations from the area of Beaufort, North Carolina, reported a growth line such as described by Belding but forming in the fall at the time of spawning in that locality. With the support of comparatively limited studies of Rhode Island populations by Risser (1901), Gutsell suggested that the line was regularly due to spawning. Irrespective of conflicts between the accounts by Belding, Gutsell and Risser, and between the earlier and later (1958) observations on the Niantic River, there are certain basic features discernible:

1. The observations on the Niantic River populations, the examination of shells shipped in from Pine Island Sound on the west coast of Florida, from Beaufort and from several sites in New England, and the analysis of photographs in Belding's and Gutsell's papers, show that in all localities the growth beyond a ring assumes the rougher appearance described above.

2. The variations in the conditions and the season when such differentiation develops and sets off a growth ring are of secondary significance. Probably there is a basic cause operating differently in different localities and varying with the history of year classes in a given locality. This may be the renewed growth which Gutsell's data indicate as a possibility in the fall in the Beaufort area, which seemed to be operative in the early spring in 1954 and 1955 in the Niantic River but in the late spring at that site in 1958, and which Belding associates with the spring in Massachusetts. It seems unlikely that spawning is a fundamental cause of ring formation. Such cannot apply to the Niantic and Massachusetts observations and is not essential to explain the Beaufort observations.

3. Shells examined suggest that the growth line is not so distinct in lower latitudes where periodic contrasts in factors affecting growth may be less marked.

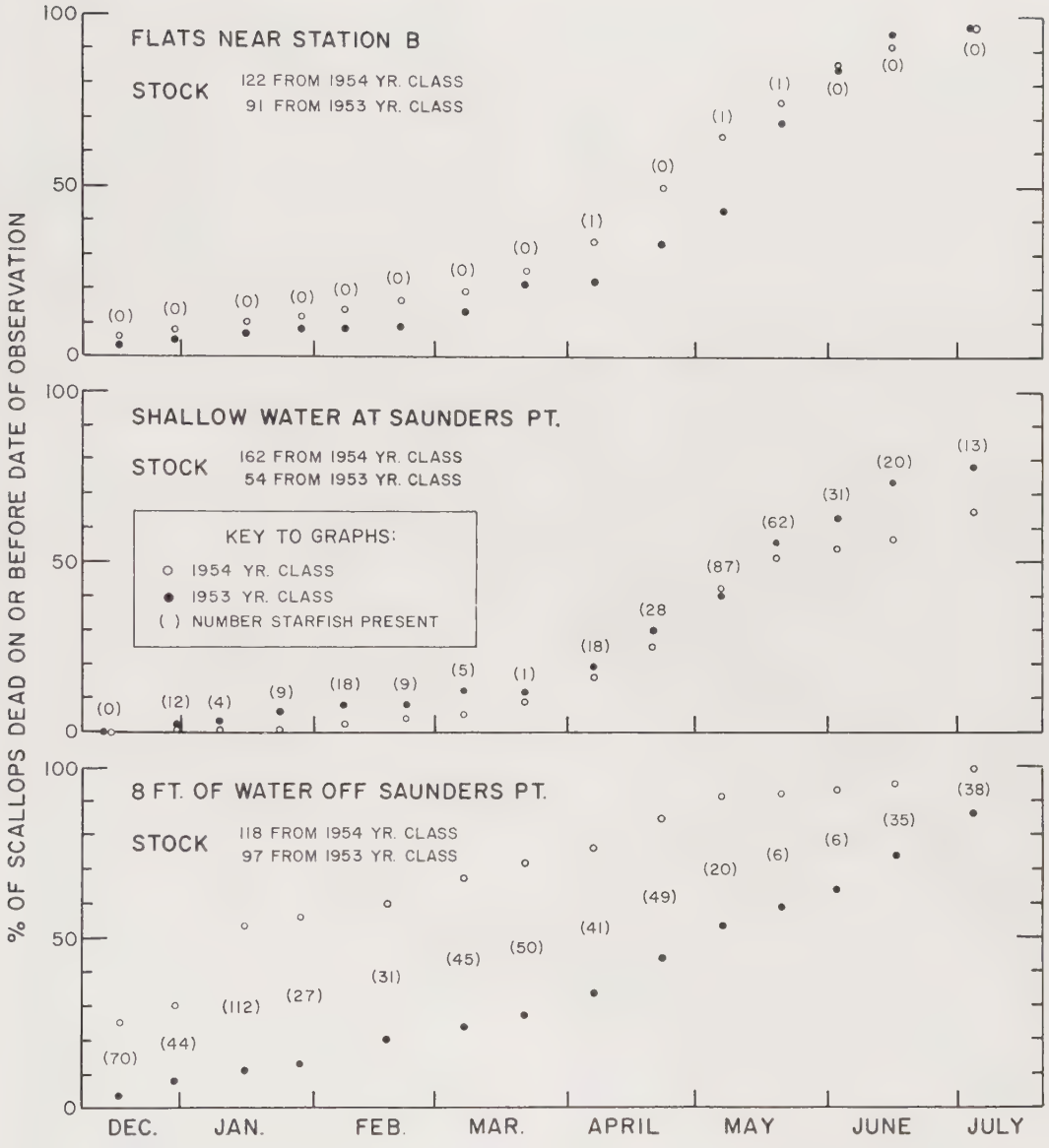

FIG. 8. Mortalities observed in caged scallops. The numbers of starfish invading the traps and removed at each observation date are given. The first oyster drills appeared in the cages on the May 19 and 20 observation dates with a total of 21 found and removed from the cage at Saunders Point from then until July 4, a total of 86 from the cage on the flats, and none in the deep water cage.

As stated in discussing Figure 6, few scallops appear to live beyond two years. During 1954 and 1955 a total of 4,143 specimens were examined from the Niantic River. Only nine of these showed two growth rings and eight of these were survivors of the 1953 year class in a sample taken from the mid-river station on July 16, 1955. Though it was reported by fishermen from Duxbury Bay, Massachusetts, that third year scallops were abundant in catches there during the 1954–55 season, a sample obtained had less than 4% with two rings. Belding (1910) also commented that relatively few scallops pass a two-year limit. He elaborated on a period of physical decline setting in after

18 months. Gutsell (1931) declined to indicate a natural life span, since in the area of his study almost the entire population of adults had been removed by fishing by the time they were 20 months old. He stated, "It is not even clear that there is any general mortality following the market season and preceding a second spawning . . . ."

Anticipating that a specific life limit would be indicated by high mortalities in the spring, I not only looked in the field for signs of decline but kept specimens of the 1953 and 1954 year classes under observation in cages. Admittedly, data on caged specimens (Fig. 8) are unreliable, for, with the water circulation cut down, the scallops did not grow well, and, in the cages off Saunders Point, predation from starfish was intense and probably exacted a heavier toll on the younger than on the older specimens. However, the mortalities of the young were everywhere heavy; even on the flats, where starfish predation was at a minimum, they died off as fast as the older specimens. In field observations I failed to observe any condition identifiable as a period of old-age mortality.

In the face of existing observations, suggestions that scallops might survive in large numbers into the third year must depend largely on the assumption that fishery intensities now prevent this. To have this effect, fishing mortality would need to be far more complete than the usual partial mortalities which diminish but do not eliminate older specimens in a population. The argument that there would be a significant survival into the third year with less intensive fishing is also countered by Figure 6, which represents collections away from the fishery area and shows a year-class mortality four to five months after the fishing season had closed.

Observations on shells from Indian middens in southeastern Connecticut have a bearing on the question of natural versus fishing mortalities, assuming that fishing pressure by Indians was at least different, if not considerably less than that of today. The shells obtained and analyed were from the following sites:

Manakaway site, Greenwich Point: collector Robert C. Suggs; 109 specimens.

South of U.S. Route 1 along west shore of Menunketesuck River, Westbrook: collectors Lyent W. Russell and N. Marshall; 233 specimens.

Millstone Point, Waterford, adjacent to highway underpass: collector Eva L. Butler; 37 specimens.

Morgan's Landing, Clinton: collectors Frank Glynn and N. Marshall; 16 specimens.

Saunders Point, Niantic, back of Adirondack log cabin: collector N. Marshall; 5 specimens.

Tubb's field, Niantic: collector Richard J. Porter; 4 specimens.

Neck Fields off Neck Road, Clinton: collector Frank Glynn; 6 specimens.

Heckler's site, Westbrook: collector Frank Glynn; 3 specimens.

From every site there was one or more scallops that showed second-year growth but none of the shells had surface features indicative of third-year growth. Though skewed by limited and selected sampling, the size-frequency distributions indicated year classes in the size range of those currently taken in the Niantic River. Two collections were large enough to permit plotting readable length-frequency graphs. For the Manakaway site the second-year scallops ranged from 1 15/16 to 3 inches with a peak and median at 2 3/8 inches, whereas the first-year scallops, only seventeen in number, overlapped this curve with a range from 1 7/8 to 2 3/16 inches and a median at 2 1/8 inches. For the Menunketesuck site, the collection was almost entirely of first-year specimens. These ranged from 1 3/8 to 2 7/16 inches with a median at 1 7/8 inches.[5] From Menunketesuck the two shells that had second-year growth and were sufficiently intact for full measurement were 2 7/8 and 3 inches. Obviously, when the Indians were fishing first-year scallops (a practice illegal today and commercially impractical because of the small return for the shucking

[5] Such data from the Manakaway and Menunketesuck sites, when compared to present length–frequency data as in Figure 6, suggest that the Indians were fishing these first year scallops in the winter.

TABLE 3. *Summary of K for one-year-old scallops collected from the Niantic River between Nov. 4 and Dec. 12, 1954*

Sampling area	Number measured	Size range inches	Mean K	Standard deviation	Current characteristic of sampling area[1]
Mid-River off Saunders Point	40	2 5/16–2 3/4	25.2	1.76	weak
Horse Point	31	2 1/8–2 5/8	25.2	2.43	weak
West shore near Station G	46	2–3 1/16	26.1	2.75	weak
Near shore at Saunders Point	25	2 1/16–2 15/16	26.9	2.03	weak
Sand bar near Station F	28	2–2 15/16	27.9	2.60	intermediate[2]
Channel between Stations B and C	22	2 3/16–2 7/8	28.5	3.07	strong
Flats toward west shore near Station B	70	2–3 1/8	28.6	2.52	strong
Flats toward east shore near Station C	29	2–3 1/8	28.8	2.40	strong

[1] Current interpretations based on observations in section titled "Niantic River."
[2] Classifying this as an area of intermediate current, in the midst of generally slack surrounding waters, is based on familiarity with the local condition and the physiographic features of the sand bar area.

effort) they sought the larger ones, and the size frequencies are skewed accordingly. Unless the Indians had some peculiar reasons to place the shells of older scallops elsewhere, a midden such as that of the Menunketesuck indicates that, at least for certain times and places, older age groups were a comparative failure. Possibly they were sometimes fished out in the first year, but this implies a harvesting intensity not generally associated with Indian times. Rather, one would expect that the Indian fishing effort was comparatively light, affording a greater opportunity for specimens to survive more than two years if such were natural.

In summary, all evidence suggests that the natural expectancy of life of the scallop in these areas is two years or slightly less. The evidence also indicates heavy mortalities throughout life and suggests that populations may show some variation in life span.

According to Belding (1910) and Gutsell (1931), rate of growth is positively influenced by the rate of the prevailing currents. Several observations on the Niantic River give support to this interpretation. As commented above, scallops did not fare well in the river when it was choked with eelgrass with little chance for circulation near the bottom. A population of unusually large seed (median size 1⅞ inches as early as Nov. 8, 1954) was found about 200 yards in from the mouth of Smith Cove in an area where tidal currents are especially strong. Experienced fishermen show a preference for working where currents are strong, simply because larger specimens are found there. The favorable effect of currents is also suggested by a preliminary comparison of muscle diameter against scallop height and the use of this as a criterion of condition. For this comparison undertaken in the fall of 1954, the muscle of the scallop was cut in half and the maximum diameter was measured. A factor K was then calculated from the relationship

$$K = \frac{\text{max. diam. of muscle} \times 100}{\text{distance as measured along curvature of right valve}^{6}}$$

Table 3 gives the average value of K for samples of scallops from different locations in the river. Specimens of less than two inches were not used in compiling this table. The higher mean values for K are found in areas characterized by strong currents, and the lower values in areas of weak currents.

It must be recognized, however, that many factors in addition to current are operative in the areas compared, and that specific cause and effect relationships cannot be deduced.

As to effects of environmental factors other than current on growth, little can be said. Within the environmental limits of areas in which scallops occur, observers have not detected favorable factors other than cur-

[6] This is the size measurement regularly used in the present study.

rent, even though the scallop occurs to depths as great as 60 ft according to Belding (1910). Seasonal variations in growth are quite simple in the northern range with the rate somewhat greater in the warm months. Figure 6 shows a slight differentiation by seasons, and Belding (1910) mentions very striking seasonal effects, though his results based on scallops in pens could be exaggerated.

SPAWNING AND SETTING

Reproductive organs were approaching spawning condition in both 1954 and 1953 year-class specimens taken from mid-river, May 18, 1955. Ripe gonads were common in both year classes when the same location was sampled on June 16 and July 16. No adequate summer sampling was done after July 16.

The time and effectiveness of spawning were observed through the use of surfaces on which scallop larvae might set after their planktonic larval life, which, according to Belding (1910), lasts about 10–12 days. For this, two types of cultch were prepared. One consisted of three-inch frayed lengths of manila rope that had never been treated with toxins and had been seasoned by previous immersion in salt water. The other consisted of groups of ten oyster shells strung on wire with half of the shells in each group facing upward and the alternate shells facing downward. Cultch of each type was suspended in the upper meter of water at three stations (B, D, and G of Fig. 1) along the length of the river. At the deeper stations, D and G, another set of cultch was suspended within one meter of the bottom. The cultch was replaced every four days.

Microscopic examination showed no signs of set on the rope units. The shells caught good sets on their upper sides, irrespective of whether these were the smooth inner surfaces or the rough outer surfaces. The shell surfaces oriented downward rarely showed any set whatsoever. This is in contrast to observations on Atlantic coast oysters which, although lacking such a marked preference, are in general more abundant toward the under surface of cultch provided (Nelson 1952). For each group of cultch, a count of the set is given for two shells which had their smooth surfaces pointing upwards (Table 4).

Counts show that in its early setting stages, the scallop thrives only in the upper waters. This may be because the planktonic stages are somewhat restricted to upper levels of these partially stratified waters. The data also suggest better setting toward the middle and upper reaches of the river. The gonad observations and setting history together indicate intensive spawning from mid-June well into July, a period within the mid-June to mid-August season set by Belding (1910) to cover both early and late spawning areas in Massachusetts. With the spawning period thus delimited to weeks when the two-year-olds are fading out, the spawning role of the first-year scallops becomes obvious. The fall spawning indicated by Gutsell (1931) for the Beaufort area has little bearing on these observations except to indicate the existence of regional differences.

In natural setting the scallops attached in quantities to most anything, including the frayed manila rope which had not worked effectively for the counts. It was evident that the small branching algae, observed to be very abundant throughout the river, were heavily laden with attached scallops. In this connection it is noteworthy that fishermen of the Niantic River refer to such algae as scallop grass. Though the role of vegetation in the ecology of scallops is not clearly established, it seems likely that the algae might have served adequately as a substitute for *Zostera* if the loss of the latter had created a need for suitable anchorage surface for the set.

PREDATORS AND ADVERSE TEMPERATURES

At the present we have only superficial knowledge of scallop predators in the Niantic River. Predators noted during this study were the starfish (*Asterias vulgaris*), the drill (*Urosalpinx cinereus*), and the green crab (*Carcinedes maenas*).

The three cages (Fig. 8) placed on the bottom for checking mortality rates of large and small scallops collected starfish and in

TABLE 4. *Scallop set in the Niantic River in 1955*

Counts based on two upward-facing inner or smooth surfaces of the oyster shell cultch. Numbers in parenthesis are conversions to numbers per 100 square centimeters calculated from rough measurements of each shell surface. Cultch groups indicated as "surface" had been buoyed to swing within 1 m of the surface, those indicated as "bottom" were buoyed to swing within 1 m of the bottom.

Date cultch was removed after 4 days exposure on station[1]	Lower River Flats Station B	Mid-River Station D		Upper River Station G	
	Surface	Surf.	Bot.	Surf.	Bot.
June 6, 10, 14	—	—	—	—	—
June 18	1 (1)	—	—	1 (1)	—
June 22	4 (2)	12 (10)	—	1 (1)	—
June 26	1 (1)	25 (18)	—	19 (12)	—
June 30	10 (5)	32 (23)	—	27 (14)	—
July 4	3 (3)	37 (26)	—	70 (70)	—
July 8	41 (26)	323 (216)	—	327 (408)	—
July 12	*	25 (15)	—	40 (21)	—
July 16	—	9 (6)	—	—	—
July 20	—	3 (2)	—	1 (1)	—
July 23	—	—	—	8 (5)	—
July 28	—	3 (2)	—	—	—
July 31; Aug. 4, 8	—	—	—	—	—
Aug. 13	—	—	—	1 (1)	—
Aug. 17, 21, 24	—	—	—	—	—
Sept. 1, 5, 9, 13	—	—	—	—	—

[1] Occasionally the exposure period was varied and this can be calculated by subtracting the preceding removal date from the one under consideration.
* Rig with cultch was missing on this date.

shallow water oyster drills as well. On each observation date such predators were removed. A total of 574 starfish was removed from the cage kept in 8 ft of water off Saunders Point, 317 from the cage kept just below the tide line at Saunders Point, and only 3 from the cage kept on the flats. By contrast 86 drills were removed from the cage on the flats, 21 from the inshore cage at Saunders Point, and none from the cage in deeper water. There were no seasonal variations in the occurrence of starfish; however, the drills were not observed in the cages prior to May 19.

Perhaps the green crab is the worst predator of the three mentioned. During the summer of 1955 standard traps built by the U.S. Fish and Wildlife Service were used to obtain an index of density of the green crab. Once during the first week of each month from May through October inclusive the traps, baited with fresh fish scraps, were set out for two successive one-day periods. Each of the successive daily catches was taken from the traps and counted. One trap was used on the flats near station B, one in shallow water on the sand bar near station F, and one near the west shore between stations H and I (see Fig. 1). On the first sampling early in May a total of 8 crabs was caught at the sand bar site. Otherwise the catches were entirely on the flats location, where the trap averaged 278 crabs per day with peaks of 1,024 and 1,104 early in June. John B. Glude, former chief of the U.S. Fish and Wildlife Service clam investigations, states (personal communication) that the highest takes in traps similarly operated along the Maine coast, where soft clam stocks have suffered a severe decline with the invasion of green crabs (Glude, 1955), are also of this magnitude.

Since scallops are often exposed in the intertidal zone and are typically harvested through late fall and winter by methods exposing the undersized specimens to air at low temperatures before they are thrown back, a few simple observations were conducted on exposure effects. These observations (Table 5) suggest little difference in low temperature resistance between seed and one-year-old scallops. It also appears that scallops are quite resistant to temperatures well below freezing. In fact, until

TABLE 5. *Summary of observations on scallops exposed to air at moderate and low temperatures*

Date of exposure	Air conditions during exposure	Surface water temperature	Number of scallops and duration of exposure[1]	Number dead	
				After 2 days	Final observations
12/30/54	Daylight exposure, scallops shaded. 48°F at start, dropped gradually to 44°F.[2]	43.7°F	25 seed—6 hours	0	0 at 7 days
			25 age I—6 hours	0	0 at 7 days
1/ 7/55	Night exposure. 23–24°F.	35.4°F	23 seed—½ hour	0	0 at 14 days
			10 age I—½ hour	0	0 at 14 days
			23 seed—1½ hours	0	0 at 14 days
			10 age I—1½ hours	0	0 at 14 days
			25 seed—2½ hours	0	0 at 14 days
			10 age I—2½ hours	0	1 at 14 days
			24 seed—4½ hours	10	24 at 14 days
			10 age I—4½ hours	3	9 at 14 days
1/14/55	Daylight exposure, scallops shaded. 22°F at start, rose to 31°F.	36.3°F	23 seed—3 hours	–	22 at 14 days
			25 age I—3 hours	–	22 at 14 days
1/21/55	Daylight exposure, scallops in sun. 11°F at start, 11°F at ½ hour, 14½°F at 1 hour, 18°F at 1½ hours, 39°F at 2½ hours.	28.4°F	23 seed—½ hour	–	0 at 7 days
			24 seed—1 hour	–	24 at 7 days
			25 seed—1½ hours	–	25 at 7 days
			10 age I—1½ hours	–	10 at 7 days
			25 seed—2½ hours	–	25 at 7 days
			10 age I—2½ hours	–	10 at 7 days

[1]Seed are scallops about 6 months old in these mid-winter months; age I scallops are about 18 months old by then. During exposure all scallops were placed in the normal position, i.e. with the right valve down. They were also placed this way when returned to containers in the water; however, it was common for individuals to flip or to be flipped over in the water.

[2] These were mild conditions and may be regarded as a control demonstrating the absence of mortality from exposure to air in favorable temperatures.

temperatures drop below 20°F, scallops may survive more than two hours in air.

C. L. Wheeler and John Hughes (personal communication) of the Massachusetts Division of Marine Fisheries exposed 50 adult scallops to 18–20°F temperatures. The scallops were dealt with in groups of 10, one group being returned to the water after 10 minutes, another after 20, and so on up to a maximum exposure of 50 minutes. A month later 7 were dead, 5 being from the 30-minute exposure group; also one was dead out of an unexposed control group of 12. From this and another experiment, inconclusive because of water supply failure in the hatchery used, Wheeler concurs that scallops are quite resistant to low temperatures, but he adds that prolonged exposure (3 hours or more) under conditions conducive to drying introduces a serious desiccation effect.

PRODUCTIVITY POTENTIAL OF THE NIANTIC RIVER AS SUGGESTED BY SCALLOP YIELDS

A figure of 15,000 bushels is used in this discussion to represent the average of the annual harvests, which actually fluctuate very widely (Fig. 5). With the second-year or market-sized scallops varying around a mean size approximating 2½ inches or about 2$^{3}/_{16}$ inches in dorso-ventral height (Figs. 6 and 7), there would be about 10,000,000 scallops in the average crop (calculated from counts per bushel in relation to dorso-ventral height as supplied by Belding 1910). Figure 9 summarizes determinations of the dry weight of the total fleshy parts[7] from 59 scallops. The dry weight of the "run-of-

[7] For convenience the shells were considered entirely inorganic. Actually, the shells from five scallops yielded a 1% organic residue after dissolving with HCl, showing that a minor error is introduced in disregarding the shell.

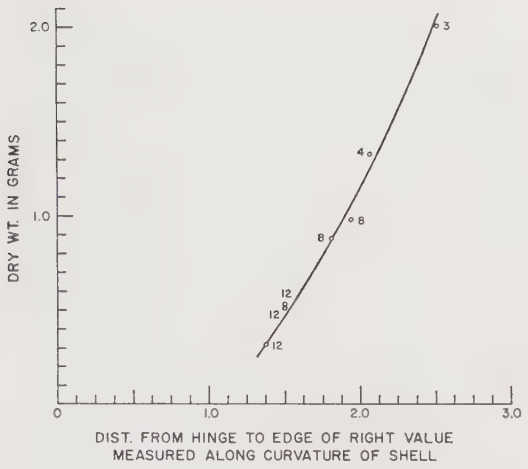

FIG. 9. Dry weight of scallop flesh in relation to scallop size. Several scallops of about the same size were grouped, their sizes were measured and averaged, and the dry weight was measured for each group and divided by the number of specimens. Numbers involved in such groupings are given next to the circles which indicate the size and weight averages.

the-crop" scallop is taken to be 1.5 grams. Thus the harvest represents 15,000,000 grams in dry weight. Considering 7% of this to be ash (Atwater 1892) and assuming that half of the organic matter is carbon, the scallop crop represents 7,000,000 grams of carbon. From the 3,196,800 m^2 basin of the Niantic River this is a yield of 2.2 gC/m^2/year. On the basis of these calculations a large crop of 40,000 bushels would yield 5.9 gC/m^2/year.

The annual harvest of scallops from Niantic River amounts to 300 lb/acre/year when calculated from wet weights. This is very high for an animal population, especially for one which is not the sole crop of a given area. A few fish produce such large crops, but this is under carefully managed conditions in small ponds without competing populations and with fertilizers added (Swingle and Smith 1941). It can be compared to the landings from Georges Bank which seldom exceed 30 lb/acre/year (Clarke 1946). Yields in beef cattle, which of course are bred as highly efficient feeders for growth without competition on grazing land, run around 150 lb/acre/year according to Graham (1944). Unlike the scallop data, the latter figures include skeletal structures.

More impressive than the scallop yields alone are the implications as to the total animal production of the Niantic River. The scallop harvest may represent far less than half the annual river production in scallops, for regulations permit nothing more efficient than hand netting from a drifting skiff, and this is not very effective in deeper water. The catch of other species utilized by man (clams, quahogs, oysters, blue crabs, and available fishes) must be taken into account also with the due recognition that the crop inevitably exceeds the take. Finally many unexploited species must contribute a major fraction of the total biota.

The key to the river's abundance probably lies in the utilization of the basic production of near-shore waters in addition to that which is endemic to the river. As discussed earlier, the mixing residual and tidal waters of the Niantic River may be thought of as a mass of water which is more or less pumped in and out with each tide. Such a water mass, by tending to retain its identity, may develop an abundance of plankton, since gains due to reproduction will not be greatly offset by dispersal (see Ketchum 1954). Furthermore the mixing that does take place in and beyond Niantic Bay is with the waters of eastern Long Island Sound which are inherently rich in nutrients and plankton (Riley 1956). Finally the tidal water moving in and out of the Niantic River is probably not subject to such heavy grazing offshore as in the river. This estuary, with its broad shallow areas and tidal circulation, causes large volumes of water to be directly exposed to expanses ideally suited for sedentary grazing populations.

The potential effectiveness of the grazing population of the river is suggested by figures provided by Chipman and Hopkins (1954) on the volume of water pumped by scallops. Applying their pumping rate figures for large and small scallops to an estimated population of 20,000,000 adults (twice the figure given above for the actual crop) and three times as many seed, one finds that the scallops alone could pump through their mantle cavities $588 \times 10^4/m^3$

in 12 hrs or about twice the tidal prism of $256 \times 10^4/m^3$.

The Niantic River can thus be considered as an effective concentrating system, utilizing production from nearshore waters as well as from within the estuary. Hulburt (1956a) has said, "Greater productivity within embayments than in the ocean may result in three ways: by enhanced conversion of inorganic nutrients, by contributions of nutrients from land drainage, and by accumulation of nutrients." To this should be added: *by efficient grazing on the plankton of the tidal prism.* The concentration action of estuaries is worthy of continued study.

A HYDROGRAPHIC CONCEPT OF THE BAY SCALLOP HABITAT

In addition to currents (shown above to be favorable for scallops), suitable bottom and water quality and a substrate for attachment of set, certain other characteristics can be defined for an estuary that is favorable for scallops. These are:

1. That the ratio of tidal volume to river flow is high, thus the salinity remains rather high.
2. That the basin is relatively shallow, with a resulting high ratio of tidal volume to the volume of the estuary at low water.
3. That the circulation is such as to retain the planktonic scallop larvae in sufficient numbers for reseeding and to provide an adequate supply of phytoplankton food, perhaps in part drawn from offshore waters or fertilized by nutrients from offshore.

It will be recognized that these are features of the Niantic River, particularly after the eelgrass had died off and permitted better circulation adjacent to the bottom (Marshall 1947). From my review of the hydrography of North Carolina sounds (Marshall 1951), I consider that these features prevail for the scallop habitats of the Beaufort area. Intense study by various workers (Barlow 1955 and 1956, Hulburt 1956a and 1956b, and Ketchum 1954) show that Great Pond, a representative Cape Cod scallop habitat, conforms to such definition. I have endeavored to check this description further through inquiries directed to other workers representing fourteen marine laboratory groups from Massachusetts through Texas and thus covering the range of this species. From information available to date, I have yet to learn of a habitat which regularly supports an abundance of scallops but lacks the first two hydrographic features listed. Obviously the third condition, stipulating a sufficient food source and conditions for reseeding, must also be satisfied, even if on a minimum basis and by means of complex hydrographic features that are yet to be understood. Though Great Pond seems like a small replica of the Niantic River, its tidal waters must be rapidly dispersed by longshore currents as they ebb into Vineyard Sound. This circulation pattern tends to disperse plankton from the lower reaches (Ketchum 1954 and Barlow 1955), yet somehow the minimum scallop food and reseeding is provided. Hulburt (1956b) has shown that some of the hydrographic features of Great Pond and similar embayments are conducive to an accumulation of plankton-producing nutrients. Ayers (1956) has shown for the clam, *Mya arenaria,* there is always the possibility that the reseeding of areas is by other than the local populations. Explanations of this sort may prove significant in offsetting the apparently adverse dispersal factors of such habitats.

The coastwide inquiry indicated that some areas seem to meet the stipulated hydrographic features yet lack scallops. Noteworthy in this respect are some of the Georgia sounds, and several sites in the Chesapeake Bay area and along the coasts of Virginia, Maryland, and Delaware. For some sites, and I can speak with greatest certainty for sites along the eastern shore of Virginia, scallops were abundant until the *Zostera* epidemic, which undoubtedly improved current conditions near the bottom but may have created a shifting, unsettled bottom condition unfavorable to scallops.

REFERENCES

ATWATER, W. O. 1892. The chemical composition and nutritive values of food fishes and aquatic invertebrates. Rept. Commissioner U. S. Commission of Fish and Fisheries for 1888, pp. 679–868.

AYERS, J. C. 1956. Population dynamics of the marine clam, *Mya arenaria*. Limnol. Oceanogr., **1**: 26–34.

BARLOW, J. P. 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. Biol. Bull., **109**: 211–225.

———. 1956. Effect of wind on salinity distribution in an estuary. J. Mar. Res., **15**: 193–203.

BELDING, D. L. 1910. A report upon the scallop fishery of Massachusetts. The Commonwealth of Massachusetts, Boston. 150 pp.

CHIPMAN, W. A., AND J. G. HOPKINS. 1954. Water filtration by the bay scallop, *Pecten irradians*, as observed with the use of radioactive plankton. Biol. Bull., **107**: 80–91.

CLARKE, G. L. 1946. Dynamics of production in a marine area. Ecol. Monogr., **16**: 321–335.

CORPS OF ENGINEERS, U. S. ARMY. 1945. Niantic harbor and River, Connecticut Review Report. Mimeo., 15 pp.

COTTAM, C., AND C. E. ADDY. 1947. Present eelgrass conditions and problems on the Atlantic coast of North America. Proc. Twelfth N. A. Wildlife Conference, pp. 387–398.

GLUDE, J. B. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Trans. Amer. Fish. Soc., **84**: 13–26.

GRAHAM, E. H. 1944. Natural principles of land use. Oxford University Press, London. 274 pp.

GUTSELL, J. S. 1931. Natural history of the bay scallop. Bull. U.S. Bur. Fish., **45**: 569–632.

HULBURT, E. M. 1956a. The phytoplankton of Great Pond, Massachusetts. Biol. Bull., **110**: 157–168.

———. 1956b. Distribution of phosphorous in Great Pond, Massachusetts. J. Mar. Res., **15**: 181–192.

KETCHUM, B. H. 1951. The exchanges of fresh and salt waters in tidal estuaries. J. Mar Res., **10**: 18–38.

———. 1954. Relation between circulation and planktonic populations in estuaries. Ecology, **35**: 191–200.

MARSHALL, N. 1947. An abundance of bay scallops in the absence of eelgrass. Ecology, **28**: 321–322.

———. 1951. Hydrography of North Carolina marine waters. Part I, pp. 1–76. *In* Survey of Marine Fisheries of North Carolina. University of North Carolina Press, Chapel Hill. 555 pp.

NELSON, T. C. 1952. Some observations on the migrations and setting of oyster larvae. National Shellfisheries Association, 1952 Proceedings, pp. 99–107.

RILEY, G. A. 1956. Oceanography of Long Island Sound, 1952–1954. IX. Production and utilization of organic matter. Bull. Bingham Oceanog. Coll., **15**: 324–344.

RISSER, J. 1901. Habits and life history of the scallop (*Pecten irradians*). Thirty-first Ann. Rept. Comm. Inland Fish., State of Rhode Island and Providence Plantations, pp. 47–55.

STEVENS, N. E., H. R. ELLIS, AND R. B. STEVENS. Wasting and recovery of *Zostera marina* on the Atlantic coast of the United States. Plant Disease Reporter, **34**: 357–362.

SWINGLE, H. S., AND E. V. SMITH. 1941. The management of ponds for the production of game and pan fish. pp. 218–226. *In* Symposium on Hydrobiology, University Wisconsin Press, Madison, Wisconsin.

U. S. GEOLOGICAL SURVEY. 1954. Compilation of records of surface waters of the United States through September 1950. Geological Surv. Water-Supply Paper **1301**: 1–380.

NOTES AND COMMENT

Oceanography vs. Fisheries

Because "oceanographers" and "fishery scientists" rub elbows in the same medium it is sometimes assumed that one is the handmaiden of the other. The thought is both inaccurate and pernicious. Koczy and Idyll (1957) have recently decried the lack of interest shown by oceanographers in supplying data that would aid in solving fisheries problems. The simple fact is that oceanographers, whether chemical or physical or biological, should not be expected to produce data satisfying the "ultimate aim" of fishery science which is described by these authors as: "to increase the yield of fish per unit of fishing effort." If the aim is really as stated, the oceanographers are being asked to locate concentrations of fishable populations, since no other activity would have so marked an effect with regard to fishing effort.

Many fishery investigators wrongly feel that hydrographic information, the plotting of oceanic currents and the measurement of basic productivity will *ipso facto* indicate where fishermen should bait their hooks. Actually, no matter how well an area is known, hydrographically or on the basis of potential productivity, it must be determined in every case that fish are actually present and catchable. At the present time, years of experience have already taught fishermen where the best fishing areas are located. It is easier and cheaper to send out experimental fishing expeditions to test old areas and locate new ones, *since this must be done in any event.*

Oceanographers are accused by the authors of "grinding out observations" without considering the "problems at hand." It depends upon who has stated the problems whether or not a set of observations are declared pertinent. Routine observations should not be ends in themselves of course. Considering the cost of modern oceanographic investigations it behooves us to take, subject to the time available, all the data that we believe will have pertinency to present or future work. The problems may take shape after data have been collected. Conversely, procedures need to be reviewed periodically to insure that inertia alone is not dictating our activities.

Of the eight examples cited as showing assistance given fisheries by oceanography only one or two are in any way connected with genuine oceanographic investigations. Nearly all involve purely biological investigations, particularly studies of animal behavior. Both Dietrich and Kalle (1957) and Tait (1952) give excellent examples of how oceanographic data have been used in interpretating changes in fish abundance and distribution.

Oceanographers can help fishery investigators understand why the fishing is not as good as they think it should be, or is not as good as it used to be. Tait (1952) states that, "there seems little room for doubt, therefore, that not only do the essential causes of fishery fluctuations lie in hydrographical conditions, . . . , but that adequate observations of these conditions affords the surest means of anticipating these fluctuations." Whether true or not, such observations are undertaken largely for the purpose of planning regulatory measures.

The types of problems that oceanography endeavors to solve are usually large scale and long term. The results can usually be applied in understanding fishery problems but this should not be made an end in itself. Special problems call for special investigations. As a matter of fact, most governmental and regulatory agencies do much of their own dirty work without attempting to justify their aims as theoretical or esoteric.

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References

Dietrich, G., and K. Kalle. 1957. Allgemeine Meereskunde. Gebrüder Borutraeger, Berlin. 492 pp.

Koczy, F., and C. P. Idyll. 1958. Oceanography and fisheries. Proc. Gulf and Carib. Fishr. Inst., **10**: 107–112.

Tait, J. B. 1952. Hydrography in relation to fisheries. Edw. Arnold, London. 106 pp.

Failure of an Anchovy to Hatch With Continued Growth of the Larva

Eggs and early larval stages of the anchovy, *Engraulis mordax* (Girard), are being investigated to determine hatching time with respect to temperature and rate of growth of early larvae. The study of larval growth rates was undertaken in order to determine the mechanism involved in the high mortality rates of larval marine fishes (See Sette 1943 and Ahlstrom 1954). The methods used in this study are described by Farris (1959).

Anchovy eggs were taken with a plankton net in the mouth of San Diego Bay on the morning of January 26, 1959. Penicillin (50ppm) and streptomycin (50ppm) were added to the incubation bottles in order to inhibit bacterial growth. Since the blastodisc was well developed (similar to the illustration by Bolin 1936, Fig. 79 stage C), it was assumed that the eggs were spawned the previous night. About two and one-half days after the assumed spawning time, 35 of the 36 eggs had hatched. The temperature had been held constant at 14°C.

The one anchovy egg that failed to hatch, appeared to develop in an otherwise normal manner. The criteria used for normal development were in agreement with the epigenesis as described by Bolin (1936) and homogeneity of embryological events among the 36 specimens examined. At no time prior to the hatching of the other eggs did the egg under discussion appear to differ from the other 35 specimens. Mr. George Mattson of the U.S. Bureau of Commercial Fisheries has observed similar anchovy hatching failures in the laboratory (personal communcation).

After the normal hatching time, the optic vesicles, fins and other body parts of the "imprisoned" anchovy appeared to be normal when compared with the "free" larvae examined at the same time. The pectoral fins and body pigmentation of the imprisoned and free anchovies appeared at the same time. The imprisoned specimen grew in length inside the egg, the body becoming greatly coiled within the egg membrane. The yolk of the imprisoned larva disappeared at the same rate as that of the free larvae. The yolk in all specimens was used up between 5½ and 7½ days after spawning. After the yolk was gone all the larvae died, as was expected, since no attempt was made to feed them.

I suspect that the failure to hatch was the result of the failure of the hatching enzyme. The function and action of this enzyme in salmon is discussed by Hayes (1949, pp. 283–285). According to Hayes, the hatching enzyme, which apparently is activated shortly before hatching, dissolves the egg membrane thereby releasing the larva. The threshing about of the larva within the egg apparently has nothing to do with its actual release from the egg, since the anesthetised larva has been observed to hatch in an otherwise normal manner (Hayes 1949).

Failure to hatch because of the death of the embryo is well known, but death owing to failure to hatch has not been reported for marine fishes so far as I know.

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References

Ahlstrom, E. H. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. U. S. Dept. Int., Fish and Wildl. Serv., Fish. Bull., **93**: 140 pp.

Bolin, R. L. 1936. Embryonic and early larval stages of the California anchovy *Engraulis mordax* Girard. California Dept. of Fish and Game, **22**: 314–321.

Farris, D. A. 1959. A change in the early growth rates of four larval marine fishes. Limnol. Oceanogr., **4**: 29–36.

Hayes, F. R. 1949. The growth, general chemistry, and temperature relations of salmonid eggs. Quart. Rev. Biol., **24**: 281–308.

Sette, O. E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 1. Early life history, including the growth, drift and mortality of the egg and larval populations. U. S. Dept. Int., Fish and Wildl. Serv., Fish. Bull., **38**: 237 pp.

Summer Upwelling Off the Northeast Coast of North Carolina[1]

Surface water temperatures reveal the occurrence of an upwelling of cold waters along the northeastern North Carolina coast during summer months.

Southwesterly winds prevailed in the Cape Hatteras region in July and August 1958 (U.S. Weather Bureau, 1958). Whereas southwesterly winds blow parallel to the coastline in the Ocracoke area, they blow onshore in the region just south of Cape Hatteras where the coastline runs east and west, and they blow offshore in the Nags Head area where the coastline runs northwest and southeast. In Figure 1, the solid line shows the water temperatures recorded on July 2, when southwesterly winds prevailed in this region. Where these winds blow parallel to or towards the shore, water temperature was over 25°C; but where these winds blow offshore, north of Rodanthe, water temperatures were less than 20°C. A similar distribution of water temperature was found on July 25 and July 27, after an extended period of southwesterly winds. Water at Oregon Inlet was as much as 6.3°C colder than water at Hatteras or Ocracoke Inlets, south of the Cape.

When northeast winds dominate, an entirely different pattern is found. In Figure 1, the broken line shows surface water temperatures recorded on June 24 after three days of northeasterly winds. Throughout the region temperatures were recorded of 22 to 23.5°C.

The observed temperature gradient in the region of Cape Hatteras can be attributed to water movements induced by southwesterly winds. Solar radiation and surf action would normally contribute to warming inshore waters in summer months. However, when winds push surface waters away from the coastline, there is no opportunity for a zone of warmed water to accumulate along the shore. This situation applies in the Nags Head area, near Oregon Inlet, when southwesterly winds prevail. In contrast, south of Cape Hatteras, onshore winds encourage the development of a zone of warm water along the shore. The water moved by offshore winds in the Nags Head area is replaced by an upwelling of cold, subsurface water. Had this movement been from surface waters to the north, the incoming water also would have been exposed to the warming effects of solar radiation and surf action, and there would not be such a marked gradient of surface temperatures in the region. Similarly, any contribution of estuarine water to this area, from either Oregon Inlet or Chesapeake Bay, would be expected to diminish any temperature gradient, for shallow, estuarine areas are typically warmer than ocean waters at this time of the year in the northern hemisphere. The only satisfactory explanation for the observed conditions involves the replacement of surface waters along the coastline by colder, subsurface waters.

Northeast winds, on the other hand,

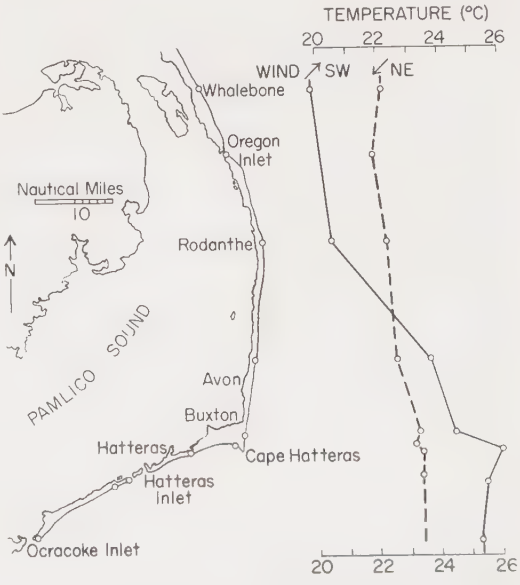

Fig. 1. Relation of water temperature to wind direction, northeast coast of North Carolina. Solid line connects observations during southwest wind; broken line connects observations during northeast wind.

[1] This work was supported by the Cape Hatteras National Seashore of the National Park Service, and by a grant from the National Science Foundation (G-5838).

would permit the development of a zone of water warmed by surf action and exposure to air along the shoreline north of Cape Hatteras, and discourage the development of such a zone south of the Cape where the wind would be offshore.

Although Parr (1933) found evidence for a sharp winter temperature gradient in the vicinity of Cape Hatteras, there was no evidence for a similar gradient in these waters in summer; instead, there appeared to be a continuity of summer temperatures extending from Cape Cod to Cape Canaveral. However, because Parr's data were collected at lighthouses and lightships (the former usually located near protected inshore waters and the latter located in deeper offshore waters), this upwelling and temperature gradient would not have appeared in his records. The present report is based on temperatures recorded along the open beach.

Littoral organisms in all but protected, estuarine habitats would be exposed to this temperature regime. By presenting an effective barrier to the extension of stenothermal species around the Cape region, this summer temperature gradient contributes to the separation of the Carolinian and Virginian faunal provinces in the Cape Hatteras region. A similar movement of water described by Green (1944) near Daytona Beach, Florida, just north of Cape Canaveral, probably provides a similar environmental barrier between the Floridian zoogeographic province, lying south of Cape Canaveral, and the Carolinian province.

A similar occurrence of cold water has been reported in the daily press (Baltimore Evening Sun, Nov. 4, 1958) for locations on the coast of Maryland and New Jersey where the cold water conditions distressed local chambers of commerce in 1958. In view of the prevalence and intensity of southwest winds in weather records for the Cape Hatteras region—six months of the year over an eight year period (U.S. Weather Bureau, 1958)—this upwelling is a normal occurrence and not an exceptional phenomenon that coincided with the dates of our hydrographic collections.

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REFERENCES

GREEN, C. K. 1944. Summer upwelling—northeast coast of Florida. Science, **100**(2607): 546–547.

PARR, A. E. 1933. A geographic–ecological analysis of the seasonal changes in temperature conditions in shallow water along the Atlantic Coast of the United States. Bull. Bingham Oceanogr. Coll., **4**: 1–90.

UNITED STATES WEATHER BUREAU. 1958. Local climatological data. Cape Hatteras, North Carolina, 1958.

NATIONAL SCIENCE FOUNDATION GRANTS

The National Science Foundation announces that the next closing date for receipt of proposals for support of renovation and/or construction of graduate level (doctoral) research laboratories is March 1, 1960. Proposals received prior to that date will be reviewed during late spring and early summer. Disposition of approved proposals will be made during late summer 1960. Proposals received after the March 1, 1960 closing date will be reviewed following the next closing date which is expected to be September 1, 1960.

This program will continue to require at least 50 per cent participation by the institution with funds derived from non-Federal sources. Proposals may be submitted for modernization or construction of research laboratories, including laboratory furnishings but not including apparatus or equipment, in any field of the natural sciences. For the present, this Program is restricted to those departments which have an on-going program leading to the Ph.D. degree. Support of facilities to be used primarily for instructional purposes will not be

considered. It is suggested that, depending on the discipline involved, preliminary inquiry be made to either the Division of Biological and Medical Sciences or the Division of Mathematical, Physical, and Engineering Sciences, National Science Foundation, Washington 25, D.C. Information concerning the Program and instructions for preparation of proposals may be obtained upon request.

In connection with its programs for the support of basic research, the National Science Foundation for some years has followed the policy of permitting institutions to apply for and receive, as an indirect cost allowance, up to 15% of the total direct costs involved in approved grant proposals.

Because of rising costs of administration and the adverse effect of such increases upon the ability of institutions to carry on research work, the Foundation has made a revision in its indirect cost policy.

Pending completion of a study of the entire problem of indirect costs, the Foundation herewith announces that, effective January 1, 1960, it will permit institutions to request up to 20% of total direct costs as the allowance for indirect costs in research proposals. In no event, however, may such indirect costs exceed the last "audited" or "negotiated" rate approved for the institution by a Federal agency for purposes of Government-sponsored research and development.

Thus, an institution with an "audited" or "negotiated" indirect cost rate so approved may claim such rate provided it does not exceed 20 per cent of the total direct costs.

This announcement will be reflected in the forthcoming revision to the 1955 edition of the National Science Foundation brochure on "Grants for Scientific Research."

Occasional Papers of the C. C. Adams Center for Ecological Studies

The first number of a new series, Occasional Papers of the C. C. Adams Center for Ecological Studies, will appear in late 1959 or early 1960. Persons or organizations interested in being placed on the Center's mailing list should write to the Director, C. C. Adams Center for Ecological Studies, West Michigan University, Kalamazoo, Michigan.

BOOK REVIEWS

STOMMEL, HENRY. 1958. **The Gulf Stream:** a Physical and Dynamical Description. University of California Press and Cambridge University Press, x + 202 pp., 82 figs., 8 tables. $6.00.

Oceanographers in particular, and all those interested in the physics of the ocean in general, will certainly welcome this excellent summary of the history, the observed features and the modern theories of the Gulf Stream system. Stommel employs his appealing informal style and clarity of exposition, so common in his many published works, to capture and build the interest of his readers. The book opens with an historical account of the early ideas and explorations of the Gulf Stream up through the last half of the nineteenth century. This concise but vivid account is drawn from an earlier paper by Stommel, a paper which must have inspired Stommel to the ultimate task of preparing the present text.

A concise but adequate discussion of the general features of the North Atlantic circulation and the physical and thermal structure, illustrated with such plates as Montgomery and Pollak's analyses of density structure, serves as useful background to the detailed discussion of the Gulf Stream which follows. Stommel has drawn heavily on the published works of Fuglister, Iselin, Worthington and others in gathering the truly pertinent observed features of temperature, salinity and density structure in various vertical sections across the Gulf Stream and the Florida Current. The material also includes charts depicting the seasonal changes in mass transport of the Florida Current (as inferred from observed fluctuations in electrical potential across the Florida Straits) and the meanders in the Gulf Stream as deduced from the Multiple Ship Survey in 1950 off the Grand Banks area.

In presenting the material on the Gulf Stream meanders, Stommel is careful to point out that several different interpretations of the basic data are possible. Because of such difficulties inherent in the paucity of suitably detailed data, little is really known about the Gulf Stream meanders other than that they do exist. This together with the notion of the fluctuating strength of the stream represents one of the more challenging problems to both empirical and theoretical oceanographers alike. But as emphasized by Stommel, before we can adequately explain these phenomena we must certainly obtain a more complete description of them. To this end Stommel argues for the well-planned long-term survey, interspersed with special tests based upon existing notions as to the mechanisms involved in the dynamics of the ocean.

After a brief chapter dealing with the shortcomings of our knowledge of the stress exerted by the wind on the ocean, Stommel launches into the discussion of the various modern theories of the Gulf Stream (and the ocean circulation in general). This rather comprehensive and well-organized summary of the more important theories (covering a span of some 50 years) is contained in five chapters of suitably simplified mathematical development amplified by discussions of the physical concepts and adequately interspersed with graphs depicting the primary results of the various theoretical models. The first two of these five chapters are devoted to the steady state theories wherein the Gulf Stream and the associated circulation of the North Atlantic are visualized as quasi-permanent, wind-driven features of the ocean. In the two following chapters the various transient state theories are discussed, insofar as these have a bearing on the meanders and variations in strength of the Gulf Stream. As in the previous two chapters, the Gulf Stream is regarded as deriving its energy ultimately from the wind via the energy input reservoir of the broad North Atlantic.

In the subsequent and final chapter dealing with the theory of currents, some hypotheses and their consequences relevant to the role of the internal circulation associated with thermohaline processes are presented. Stommel admits that these latter considerations, his own latest contribution to the subject, are somewhat speculative. The exciting feature of Stommel's thermohaline theory (expanded upon in his subsequent publications) is the prediction of a sluggish but persistent deep undercurrent beneath the Gulf Stream. This feature has been partially verified by Swallow and others since the preparation of the original manuscript of the book. It yet remains however, to explain the geographical structure and magnitudes of the field of vertical velocity which is demanded in Stommel's thermohaline theory.

In his review of the steady state theories of currents (since the pioneering work of Ekman), Stommel distinguishes clearly between the so-called linear (viscous) theories and the non-linear (inertial) theories, particularly as pertain to the Gulf Stream and its sister phenomenon—the Kuroshio Current—in the Pacific. The earliest theories (those of Rossby, Stommel, Munk and Stockmann (assigned a sufficient role to lateral and/or bottom friction in the balance of torque on a column of sea water. The Sverdrup theory of wind-driven current in the equatorial Pacific did not require lateral friction in order to achieve realistic results and it was soon recognized by Munk and Carrier that the Gulf Stream could be regarded as a boundary-layer phenomenon containing virtually all of the frictional torque required in the balance of the external wind torque exerted on the North Atlantic as a whole.

The most recent theories of the Gulf Stream (those of Morgan and Charney) regard the latter

phenomenon as an inertial boundary-layer, wherein frictional effects are not considered explicitly. From a mathematical point of view one is confronted with the task of solving non-linear partial differential equations in the inertial theories, while in the viscous theories one arbitrarily absorbs the effects of advection of momentum (inertial effects) into the higher order but linear viscous terms and thereby introduces an unknown parameter (the eddy viscosity) into the system of equations. It is apparent that Stommel favors the inertial theories of the Gulf Stream over the viscous theories even though both give a qualitatively good picture of the phenomenon. However, in spite of the more physically sound approach of the inertial theory, there is an inconsistency which Stommel does not emphasize. The Morgan-Charney steady state inertial theory does not provide a mechanism for the balance of the integrated external wind torque applied to the North Atlantic. If viscous effects are rejected, it is still possible to have a lateral form drag due to differences of pressure at different parts of the irregular coast as Stommel points out. However, I cannot see where this phenomenon is allowed for in the existing theories. On the other hand the kinetic energy dissipation which is required in order to balance the energy input due to winds over the whole North Atlantic could be accounted for by introducing an energy sink at the point of breakdown of the Morgan-Charney regime of inertial flow. Presumably this occurs in the region of the meanders.

Stommel indicates by perturbative methods as applied to a simple mathematical model, the condition under which stationary unstable meanders may develop. This criterion turns out to be the condition of critical internal Froude flow, as anticipated by Rossby in analogy with the hydraulic problem of critical river flow. From a mathematical standpoint it appears that the perturbations of the stream must be strongly coupled with the mean zero order state of flow, via the non-linearity of the problem, if the perturbations are to exert an important role in robbing energy from the mean flow; furthermore this must be largely an irreversible process of energy transfer. If we imagine such energy transfer occurring continuously through smaller and smaller scales of motion within the meander region then ultimately the energy can be dissipated through the action of real viscosity processes at the microscale level.

The seasonal fluctuations in the Gulf Stream are discussed by Stommel in the light of recent theories advanced by Ichiye, Veronis, Morgan and Stommel, relevant to the response of the ocean to fluctuations in the wind field. The Veronis-Stommel theory in particular predicts that changes in the wind field having a period of a week to a year will cause a barotropic response of the ocean which is essentially in equilibrium with the applied wind field on any particular day. This cannot be tested by observation of density structure alone since changes in the latter do not reflect the changes in the barotropic field of pressure. However, by employing water level data corrected for thermohaline effects, the barotropic response can be estimated. Stommel shows that the seasonal changes in the barotropic response compare favorably with that predicted from seasonal changes in the wind torque over the North Atlantic.

The book is a vivid presentation of the really significant features of the Gulf Stream and a clear exposition of the author's philosophy in respect to the field of physical oceanography in general. Some of the most significant advances in our knowledge and understanding of the Gulf Stream and the associated circulation of the North Atlantic have occurred only in the past ten years. The progress has been so rapid in fact that many of the newest findings were added to the text after the original manuscript had been completed. Unfortunately some of the more recent work on meanders by Saint Guily and others could not be included. Stommel has selected those theories for discussion which seem to be best supported by the observed phenomena, or which, because of their pedagogical nature, would warrant inclusion in the text. He has obviously striven to summarize the presented material in sufficient detail to give the reader a clear idea of the merits and possible shortcomings of the various hypotheses and of the observational material at hand. The reader should be encouraged by the progress which has been made in our understanding of the dynamics of the ocean currents and he will be delighted at the apparent ease with which Stommel is able to get to the heart of the problem and to convey this understanding.

In his concluding remarks, Stommel offers us considerable food for thought in his statement directed to the oceanographic mathemagician: "Too much of the theory of oceanography has depended upon purely hypothetical physical processes. Many of the hypotheses suggested have a peculiar dream-like quality; and it behooves us to submit them to especial scrutiny and to test them by observation."

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Wieser, Wolfgang. 1959. **Free Living Nematodes and Other Small Invertebrates of Puget Sound Beaches.** University of Washington Press, Seattle. vii + 179 pp., 111 figs., 46 pls. $4.20.

This publication is well organized and illustrated, the number of individual figures in the plates being considerably larger than indicated by the numbers given above since the majority of figures (with the notable exceptions of figures 1 and 109) are multiple, various parts of the body of the organisms

illustrated carrying designations such as 31a, 31b, and 55a, 55b, 55c, 55d, 55e, and 55f. The illustrative work is neat and appears to be well done. In addition to ten larger numbered tables, there are five short non-numbered tables in the Introduction and some of the information in the taxonomic descriptions is given in short tabular form. The major headings in the body of the article are: Introduction (pp. 1–6); Part I: The Taxonomy of the free-living nematodes (pp. 7–97); Part II: Distribution of species, with ecological remarks (pp. 99–117); Plates (pp. not numbered but apparently meant to be pp. 119–166); Bibliography (pp. 167–172); and Index (pp. 173–179). The index is strictly one of scientific names of the genera and species of animals and plants mentioned in the text, those reported from Puget Sound being underlined. In a six-line preface to the actual index, the author distributes the credit for the taxonomic identifications of Cumacea, Copepoda, Polychaeta, Isopoda, Chelifera, Amphipoda and Ostracoda, accepting the responsibility himself for the identifications of Nematoda, Gastrotricha, Hydrozoa, and Archiannelida.

In the Introduction, a statement is made of the previous publications on the various groups discussed from the West Coast of North America and citations are given to many other publications on the marine "nematodes" from the East Coast of North America. There are also acknowledgments of assistance in the work presented here and brief discussions of work previously done elsewhere, with comments on the problems involved, and a brief discussion of salinity with the definitions of the classification of types of water on the basis of salinity by Välikangas (1933): "marine water >30‰; polyhaline water = 15–30‰; mesohaline water 3–≈15‰; and oligohaline water 0.5–≈3‰." Mesohaline and oligohaline waters are termed "true brackish water." Temperatures of the surface waters of Puget Sound are reported as 14°C in summer and 8.5°C in winter. Tides (mean and diurnal ranges at Seattle of 7.6 and 11.3 ft resp., with highest and lowest tides 14.8 and –4.5 ft) are reported. Localities (5) in the area investigated with sample numbers, intertidal heights, average grain size, and collection dates are presented in tabular form with short discussions, which include mention by generic and sometimes specific name of the various dominant ecologic forms in each of the beach habitats.

Part I. Consists of the taxonomic descriptions of the "free-living nematodes" encountered, with their local occurrence and remarks, as well as, some taxonomic discussion. Three new genera are described, 75 new species, and one new "variety," two forms are described as *sp*; 33 old species are redescribed and two additional old species are reported. Keys are provided to the species of 11 of the 62 genera reported. This section appears to be properly organized and the author places to Family the genera and species reported. This is in marked contrast with his previous publications which have been organized and presented according to "Order" as well as Family. Considering the fact that the systematic placement of all "nematodes" is presently undergoing a severe re-evaluation and many new ideas in classification and groupment are appearing, the chief "revolutionaries" relative to the classification of the marine nemas being Dr. G. S. Gerlach and Dr. Wolfgang Wieser, it is the present reviewer's judgment that omission of the ordinal ranks during the present rather chaotic period of reshuffling is a decided improvement since he has been unable to understand their concepts of the various orders without new diagnoses which the authors mentioned have appeared to be unready to provide. Such is understandable when many genera and families have been shifted from Order to Order and the task is as yet incomplete. These authors apparently recognize the faults in present systematic arrangements (as does the reviewer) and may well, along with the reviewer. be searching for new and better concepts and have not yet been able to assemble the necessary information to present a completely new comprehensive classification of the groups concerned.

It was for precisely this reason that the reviewer accepted with pleasure the ruling of the XVth International Congress on Zoology (London—July, 1958), that removed the names of all taxa above the Family-Group from the jurisdiction of the International Commission on Zoologic Nomenclature. According to the London revision of the International Rules of Zoologic Nomenclature, names of taxa from Subspecies to Superfamily are subject to the International Rules while those names of taxa above the rank of Superfamily (Order, Class, and Phylum) are not since these higher taxa are considered to be too subjective (theoretic) to be "frozen" in our present state of knowledge. Preservations of the stems of the names of many of the higher taxa currently in general use might well contribute more to confusion than lead to stability in groups which are undergoing or have undergone revolutionary revisions in systematic concept. This state is so marked at present among workers on the systematics of marine nemas that the present reviewer plans to omit the ordinal rank in his own publications on marine nemas.

In the present article, Wieser places his genera and species to family but gives no diagnoses of the families, no keys to the genera of the included families, no diagnoses of the majority of the genera and no keys to the species of the majority of the genera. However, references are supplied to other articles which contain keys to most of the genera and species. The absence of keys to families, genera, and species in the present article, combined with the absence of diagnoses of families and genera may be considered an objectionable feature in the article by students not already familiar with the taxonomy of marine nemas. However, the illustrations are well done and should serve as excellent guides.

Part II which contains the author's observations on the ecologic distribution of marine organisms

including Hydrozoa, Nematoda, Gastrotricha, Archiannelida, Polychaeta, Copepoda, Ostracoda, Cumacea, Amphipoda, Chelifera, and Isopoda contains tables giving by species the "Horizontal Distribution" and "Intertidal Distribution" of the animals collected. The discussion also notes type of bottom (median particle sizes of 75 to 420μ, pl. 46, fig. 109) and comments on possible occurrence of particular species in given substrates being a function of particle size.

The publication is unquestionably a major contribution to knowledge about the species occurring on the Western Coast of North America and contains little theoretical discussion which might be subject to criticism. While the price postpaid ($4.20) seems, to the reviewer, rather exhorbitant, that is not the fault of the author and the publishers may find it will discourage sales to the younger students and they may be forced to reduce the price, which is, fortunately, not printed in the publication.

B. G. Chitwood

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PROCEEDINGS OF THE AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY, INC.

22nd Annual Meeting

University Park, Pennsylvania

September 1, 1959

The meeting was called to order by President W. E. Ricker at 11:05 A.M.; seventy-five members were present. The minutes of the 21st annual meeting were approved as printed in LIMNOLOGY AND OCEANOGRAPHY, Volume 4, Number 1.

In the President's report, Dr. Ricker told of the resignation of Dr. D. G. Frey as Editor at the end of a 3-year term, and the appointment of Dr. K. M. Rae to this position by the Board of Directors. The transfer of responsibility from Dr. Frey to Dr. Rae occurred early in 1959. Dr. B. H. Ketchum moved that an expression of appreciation for his years of service as editor be sent to Dr. Frey. The motion was seconded by Dr. I. E. Wallen and passed unanimously.

The standing committees, with rotating membership, which functioned during 1959 were as follows (last year of each individual's term of office is indicated):

Apparatus and Supplies Committee:
John H. Ryther, Chairman (1959)
G. H. Lauff (1959)
C. S. Yentsch (1960)

Identification Service Committee:
J. W. Hedgpeth, Chairman (1960)
J. L. Brooks (1959)
N. V. Wilimovsky (1961).

Special Committees appointed for the year 1959 were as follows:

Auditing Committee:
F. F. Hooper
J. W. Moffett

Nomination Committee:
J. L. Hart (Chairman)
D. F. Leipper
T. C. Nelson

Tellers:
A. M. Beeton
J. H. Johnson

Committee on 1962 International Limnological Congress:
A. D. Hasler (Chairman)
Advisers as required

Committee on NSF Travel Grants for Attendance at the 1959 Congress of Limnology in Austria:
D. C. Chandler (Chairman)
W. T. Edmondson
H. T. Odum
Ruth Patrick
D. S. Rawson

Committee on Costs of Publication:
F. F. Hooper (Chairman)
G. H. Lauff
H. T. Odum
K. M. Rae

Joint Committee on Aquatic Biology (Ecological Society of America and ASLO)
B. H. Ketchum (Chairman)
H. H. Carriker
G. L. Clarke
E. W. Fager
D. G. Frey
A. D. Hasler
H. T. Odum.

Representatives of ASLO to other organizations or for special purposes were as follows:

National Research Council	L. A. Walford
American Institute of Biological Sciences	B. G. Anderson
National Resources Council	T. H. Langlois
American Association for the Advancement of Science	W. L. Schmidt
ASLO representative for arrangements for the 1959 Annual Meeting at State College	E. L. Cooper
Consultant from ASLO to AIBS in revising their "Specialties List"	G. L. Clarke.

It was announced that the regular meeting of ASLO in 1960 will be with AIBS at Oklahoma State University, Stillwater, Oklahoma. The 1961 meeting will also be with AIBS, either at the University of Illinois or Purdue University. During these years, two special meetings will be held at centers of aquatic research. They are to emphasize oceanography and particularly physical oceanography, but will not be restricted to these fields.

The President reported that no Library Subscription Committee had been appointed, but that he had personally been in touch with about 100 libraries, soliciting subscriptions on behalf of the Society. Similarly, no Membership Committee was appointed on the theory that all members should act in that capacity and from time to time actually do so; the President, himself, had approached about 100 individuals during the year, with some success.

At the 1958 meeting it had been moved that a Committee be appointed to list translations of papers in foreign languages and arrange for their reproduction. No action was taken in 1959 because it seemed it would duplicate the activity in this field of the Office of Technical Services of the Department of Commerce in the United States, and the National Research Council in Canada.

The report of the Secretary-Treasurer was presented by Dr. F. F. Hooper, in the absence of Dr. G. H. Lauff. He reported that during 1958–59 (since the last report) 98 members had joined the Society, of whom 93 are active members and 5 are associates. During the year 20 members resigned, and 39 were suspended for non-payment of dues. Total paid membership, as of August 14, 1959 was 865, of whom 17 are associate members and 15 are emeritus members. The number of non-member subscriptions to the journal has increased to 298, as compared with 217 a year ago.

There was some discussion of the financial situation faced by the Society, and the measures to be taken to ensure stability in the future. Dr. George Sprugel reported that the full amount of the 3-year NSF publication grant had been allowed. Dr. Ketchum moved that the Secretary-Treasurer's report be accepted; the motion was seconded by

Dr. L. A. Krumholz and was passed unanimously. The Editor, Dr. Rae, discussed the backlog of papers for publication in LIMNOLOGY AND OCEANOGRAPHY.

Dr. Hooper presented a report of the Special Committee on Publication Costs. The Committee recommended that the Society print LIMNOLOGY AND OCEANOGRAPHY at Allen Press, Lawrence, Kansas, beginning with Volume V, Number 1. It anticipated a saving of about $2,000 a year as a result.

Dr. J. H. Ryther reported on the revised apparatus and supply list. He indicated that most of the cost of manufacturing of this publication was met by the concerns listed in it.

Dr. Ketchum read the report of the Joint Committee on Aquatic Biology (Ecological Society and ASLO).

Dr. B. G. Anderson reported on the actions taken by the Executive Committee of AIBS. AIBS has taken steps towards organizing a publication agency, which should be of value to cooperating societies. Dr. G. L. Clarke suggested we explore the possibility of obtaining AIBS assistance in publishing LIMNOLOGY AND OCEANOGRAPHY. Dr. Ketchum pointed out that Dr. Clarke was chairman of the Committee of the Ecological Society exploring the possibility of AIBS assistance and that it would be appropriate for him to carry on the same investigation for ASLO. Dr. Ricker appointed Dr. Clarke to investigate AIBS publication services for the Society. Another item of interest is that AIBS had accepted an invitation from the University of Colorado for the 1964 meeting.

Dr. D. C. Chandler announced that 24 applicants were offered and had accepted awards for travel expenses to the International Limnological Congress in Austria, from the money furnished by the National Science Foundation.

Dr. Hooper reported on the actions of the Board of Directors at the meeting on August 31. Actions of the Board were as follows:

1. Approved transfer of a surplus of $1,008.40 in Society funds to LIMNOLOGY AND OCEANOGRAPHY, if such a transfer was desirable.
2. Authorize a change of printers.
3. Approved a budget of $10,700 for the Society (including LIMNOLOGY AND OCEANOGRAPHY) for 1960.
4. Voted to give every assistance and encouragement possible to organizations concerned with increasing oceanographical research, training, recruitment, and physical facilities along the lines of the needs outlined in the recent Committee report to the NAS-NRC. It endorsed ASLO's sending a resolution to NAS-NRC, and the appointment of a standing Educational and Recruitment Committee to take active part in furthering these aims.

Dr. Ketchum elaborated upon the action taken by the Board of Directors in regard to the NAS-NRC report on Oceanography. He presented the resolution to the Society concerning the oceanographic report that had been approved by the Board of Directors. This resolution was discussed by the membership; it was suggested and agreed that the word "some" be deleted from the first paragraph. Dr. H. T. Odum moved that the Society approve the resolution, as revised; this motion was seconded by Dr. Clarke and was passed unanimously by the Society. The text of the approved resolution is as follows:

> "The American Society of Limnology and Oceanography heartily congratulates the Committee on Oceanography of the National Academy of Sciences-National Research Council for the recognition they have given to the problems and needs of Oceanography as presented in their report entitled OCEANOGRAPHY 1960 TO 1970.
>
> "The American Society of Limnology and Oceanography concurs, both as a scientific society and on behalf of its members in the necessity of expanded programs of research in all disciplines, such as physics, chemistry, biology,

meteorology and geology as they apply to the basic problems of aquatic science.

"The Society recognizes, further, the need for adequately trained personnel if the expanded program envisaged by the report of the Committee on Oceanography is to become effective. Since the American Society of Limnology and Oceanography represents a large number of members in responsible academic positions, the Society recognizes its responsibility in connection with the necessary educational program. A standing committee, The Education and Recruitment Committee of the American Society of Limnology and Oceanography has been established for this purpose.

"The Society is willing and prepared to assist in any way possible in the effort to improve education and research in aquatic sciences."

A proposed amendment to the second Article and a new 8th Article of Incorporation were presented to the Society. Dr. Sprugel moved that the Society approve these changes. The motion was seconded by Dr. Wallen and passed unanimously.

Dr. V. D. Vladykov suggested a luncheon or dinner be held at the annual meeting.

The problem of encouraging teachers to attend meetings of the AIBS was discussed.

Dr. R. M. Darnell favored publication of abstract papers presented at this meeting. It was pointed out that the Monday symposium was being distributed by the Odum brothers to those who requested it, also that abstracts of the Wednesday joint symposium were available in the ESA Bulletin.

The results of the election of officers for 1959–60 were reported by the Tellers as follows:

President	Bostwick H. Ketchum
Vice-President	Gerald W. Prescott
Member-at-Large (3-year term)	C. M. Tarzwell
Editorial Board (3-year terms)	C. H. Mortimer; T. Braarud; L. A. Walford.

Dr. R. C. Ball moved that the Society express appreciation to the local chairman, Dr. E. L. Cooper, for his efforts in arranging the meetings at Pennsylvania State University. Motion seconded and passed unanimously.

The meeting adjourned at 12:15 P.M.

Respectfully submitted,
FRANK F. HOOPER
Acting Secretary-Treasurer

INCOME AND EXPENSE STATEMENT

January 1–December 31, 1958

SOCIETY

Income			
1958 Dues	$ 2,019.00		
Interest	111.82		
Special Publications	5.70		
Miscellaneous	6.00	$ 2,142.52	
Expense			
Addressing and Mailing	$ 65.72		
Printing	358.83		
Postage	150.36		
Secretarial	175.93		
Contributions	125.00		
Pacific Section	55.89		
Travel	176.84		
Miscellaneous	25.47	1,134.04	$ 1,008.48 cr.

JOURNAL

Income			
Volume I	$ 471.50		
Volume II	468.50		
Volume III	6,455.50		
Reprints	1,568.42	$ 8,963.92	
Expense			
Manufacture	$10,305.04*		
Secretarial	351.84		
Addressing and Mailing	316.67		
Reprints	1,485.76		
Editorial	100.00		
Miscellaneous	40.60	12,599.91*	3,635.99 dr.*
			$ 2,627.51*

* Actual cost of manufacture of Volume III was $10,305.04. Manufacturing cost applicable to income received during 1958 from sale of Volumes I, II, and III was $7,779.35.

BALANCE SHEET

December 31, 1958

Assets		*Liabilities*	
Cash	$4,257.60	Accounts payable	$ 484.25
Accounts receivable	314.90	*Equity*	
Inventory	3,890.88	Earned surplus	7,979.13
	$8,463.38		$8,463.38